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Reproduction in the Bangiophycidae.

KATHLEEN M. DREW 553

FUTURE CONTENTS
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REPRODUCTION IN THE BANGIOPHYCIDAE

KATHLEEN M. DREW

University of Manchester, England

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INTRODUCTION

After a period of comparative neglect, there has been evidence of renewed interest in the Bangiophycidae in recent years. On the whole, the writers of recent papers show an acceptance of the interpretations of the earlier workers, although first-hand acquaintance with the earlier work would show that, valuable as it is, the evidence for statements made is sometimes very scanty and at times unconvincing. A survey of the literature reveals, in addition, that, even after allowance has been made for the different periods when the observations were made, no attempt has been made to correlate the observations on reproductive bodies in one genus with those in another. Without such correlation, interpretation is bound to suffer. A résumé of the literature dealing with reproduction in the Bangiophycidae, indicating the extent of the evidence, together with a consideration of the interpretations offered by past workers in this field, is therefore timely.

Although members of the Bangiophycidae have worldwide distribution in aerial, freshwater and marine habitats, the group is a very isolated one, considered from the taxonomic and phylogenetic points of view. Reasons for assuming phylogenetical relationship with such widely separated taxa of algae as the Schizogoniales, the Cyanophyta and the Florideophycidae have been put forward from time to time by various phycologists. The nature of the pigments has been given emphasis in such discussions, but it would seem desirable that the reproductive processes and the life-history also be given considerable weight. As will be shown in this review, our knowledge of the reproductive processes and the life-history of many of these algae is very scanty; consequently the need for pre-

cise and well-documented investigations is stressed. One of the preliminaries to the establishment of the life-history of a given species is certain information about reproduction, such as what types of spores occur and whether the spores give rise to thalli similar to the thallus from which they originate. It is also essential to know where fertilization and meiosis take place. Judged on these criteria alone, the life-history of both well-known and oft-investigated Bangiophycidae, such as *Bangia* and *Porphyra,* still challenge the investigator by the number of unanswered questions they pose. The same applies with more justification to extremely rare genera, e.g., *Kneuckeria* which contains one species and, as far as I am aware, has been found once only on the Sinai peninsula in 1904.

The type of spore, as well as the manner of its formation, have been used as characters of taxonomic importance for the separation of both larger and smaller units within the Bangiophycidae. This review shows how vague our knowledge on this very important subject is at present, and no attempt seems to have been made to interpret or relate the different types of spore formation by a general survey.

The reproductive cells of the Bangiophycidae are all non-motile. Propagation in the unicellular types is effected mainly by means of vegetative cell division, and after a review of relevant observations dealing with this section of the Bangiophycidae, the multicellular types will be considered. While the most frequently described spores of these forms are considered to be asexual, sexual reproduction is reported in the following genera: *Compsopogon, Kyliniella, Porphyra, Bangia, Porphyrella, Erythrotrichia, Erythropeltis, Erythrocladia.* A review of spore formation in the multicellular types is followed by a consideration of the accounts of sexual reproduction in the genera just mentioned. Since it is not the main theme of this review, the subject of life-histories of the algae of the Bangiophycidae is only briefly considered.

The amount of available information about reproduction varies considerably from genus to genus, and, in addition, the terminology used for the reproductive cells is far from consistent. Apparently this is the result of uncertainty regarding both the interpretation of observations and the relationship of the individual alga being studied. At times, it has been found necessary to use the term employed by the investigator whose work is being described, but,

as far as possible, the term " monospore " is applied to those spores which have been designated either with this term or " gonidium " or " neutral spore ".

The names in this article are those in common use, but some of them may not be correct according to the International Code of Botanical Nomenclature.

REPRODUCTION IN UNICELLULAR FORMS

Vegetative division of the cell into two identical daughter-cells appears to be the usual method of multiplication in the unicellular forms of the Bangiophycidae. However, records of other methods of reproduction are to be found for all genera except the once recorded, monospecific genus *Rhodosorus* (Geitler, 1930).

Resting cells have been described for *Vanhöffenia* (Wille, 1924), another monospecific genus (*V. antarctica*). The walls of the vegetative cells become thickened, and on germination such resting cells give the usual vegetative cells once more. Geitler (1927, Fig. 2a) has described resting cells for the only species of *Rhodospora, R. sordida.* These are large spherical cells with a thick refractive membrane, an abundance of assimilation products but pale pigments.

Division of cells into more than two daughter-cells has been described for *Rhodospora, Porphyridium,* and *Chroothece.* Cells of *R. sordida* divide by successive endogenous walls into a number of smaller cells which are retained within the membrane of the original cell-wall (Geitler, 1927, Fig. 1; *see* Pl. I, E). Unlike normal vegetative cell division, there is little enlargement of the daughter-cells between successive divisions and no decay of the common membrane. As many as 16 daughter-cells, which Geitler calls " autospores ", may be formed within the original membrane which then ruptures, allowing them to escape. More recently Geitler (1955) has reported that as many as 32 autospores may be formed within the original membrane.

In contrast to *R. sordida,* in which the mother-cell may divide by successive wall formation, Geitler (1944) has described the simultaneous division of cells of *Porphyridium cruentum* into four daughter-cells. In the older layers of material which Geitler collected in Vienna, there were cells containing four nuclei, and he was able to watch the division of similar cells into four (l.c., Figs.

2a, 4, 5) by simultaneous division into four portions involving the chromatophore, pyrenoid and protoplast (Pl. I, D). Sometimes the resulting daughter-cells were arranged tetrahedrally, sometimes in one plane. As the membrane of the parent cell takes part in the process of division, Geitler does not consider the daughter-cells to be autospores. In Figs. 2 a and b (Pl. I, D), however, a common membrane is shown enclosing several daughter-cells, but these may have been former differently. Kufferath (1920, Figs. 5, VI, VIII, XII, XIII; 16, VI) also has figured cells of *Porphyridium cruentum* containing four or more cells within a common membrane and has expressed the opinion that the cells which divide thus are sporangial. Kufferath does not appear to have followed the division of selected cells, as has been done by Geitler, but he states that the divisions, although successive, follow each other quickly.

Pascher and Petrova (1931) also describe quadrates of cells for *Chroothece mobilis* but consider them to be abnormal. On the other hand, on the ground that they occurred too commonly to be considered an abnormality, they accept examples in which one or two thick-walled cells were bound together with exceedingly small thin-walled cells as normal. Their formation was not observed, but, since they occurred within a common membrane, it is considered that the four cells had a genetical connection. The small cells of the group usually contained a chromatophore and a nucleus but never a pyrenoid, and the authors suggest that they may be spermatia.

An observation of interest made by Geitler (1944) on *Porphyridium cruentum* concerns the cutting off of " buds " by certain cells. Protuberances may appear on cells either while at rest or in the process of division and may or may not contain a nucleus and a fragment of chromatophore, but no pyrenoid was ever found in them. Sometimes these protuberances were cut off and rounded up as small separate cells, such as can be found in naturally occurring material, but at other times they were withdrawn into the parent cell. Although these cells of *P. cruentum* appear to be able to change their shape in this " budding " process, a membrane is said to be present. If such " buds " or small cells are cut off during division of the cell into four, as indeed may happen, the result is very like the groups of large and small cells observed by Pascher

and Petrova (1931) in *Chroothece mobilis*, and the latter may have originated in the same way. Although small cells of the type cut off as "buds" were to be found in naturally occurring material, Geitler (1944, p. 315) considers their formation a pathological process.

Release of the entire contents of an individual cell as a single body has been reported for *Porphyridium cruentum* and *Chroothece mobilis*. Vischer (1935) reports that under certain conditions, active, naked, amoeboid, motile cells are formed in cultures of *Porphyridium cruentum* on nutrient agar. These cells creep on the substratum but soon become enclosed by a wall again. Their origin has not been ascertained by Vischer and hence it is uncertain whether they are to be considered as monospores or not, but, by analogy with other Bangiophycidae, Vischer suggests monospore status. The movement of these cells is possibly of a different type from that of the usual vegetative cells of *P. cruentum* with membranes (Geitler, 1944, 1953; Pringsheim, E. & O., 1949).[1]

Pascher and Petrova (1931) have described the release of the cell contents of *Chroothece mobilis* as rejuvenated cells, the release taking place through an equatorial split in the parent cell-wall.

In a culture of *Chroothece rupestris* Gayral (1952) observed cells grouped in fours, which later germinated to give branched septate filaments containing parietal plastids. The filaments formed hooks and protuberances, thought by Gayral to be the place of origin of the young thalli which appeared in the culture a few months later. The investigator interpreted the cells grouped in fours as carpospores, and the filaments to which they gave rise as protonema, on which the new thalli developed, comparing the process to that described by Dangeard (1931, 1933) for species of *Porphyra*.

[1] Movement of the vegetative cells of *Chroothece mobilis*, borne at the end of well-defined stalks of mucilage, has been described by Pascher and Petrova (1931). (Cf. isolated cells of *Asterocytis smaragdina* Rosenberg, 1935.)

REPRODUCTION IN MULTICELLULAR FORMS [2]

Classification of Types of Spore Formation [3]

In attempting to classify the types of spore formation in the multicellular Bangiophycidae, considerable difficulty has been encountered. Apart from the great variety of terminology in use, there is a serious lack of precise information regarding the method of formation of the spores and in some instances of the mother-cell or sporangium as well, e.g., the microaplanospores of *Compsopogon*. In addition, it is not always easy to differentiate between purely vegetative divisions and the first division of a potential sporangium; this has undoubtedly led to discrepancies in the accounts. Also, while it is clear that certain spores are purely asexual, others are considered by some to be sexual in origin and are referred to as "carpospores". Proof for this interpretation depends partly on correctly recognizing the female gametes; the difficulty of doing so is pointed out in the section dealing with the accounts of sexual reproduction. Therefore, in the classification of types of spores which now follows, no attempt has been made to distinguish between asexually and sexually produced spores. They are classified according to the method of formation of the mother-cell, or sporangium, and according to whether this divides to liberate more than one spore or whether the entire contents are liberated as a monospore.

As a result of a survey of the literature, the following classification of types of spore formation is proposed. The distinguishing characteristics of each type are given briefly and examples listed. This is followed in the subsequent pages by fuller descriptions of these examples, together with information about the method of liberation of the spores, their behaviour after liberation and their method of germination.

[2] The distinction made between unicellular and multicellular forms is somewhat arbitrary and hence some of the genera grouped here show as close a relationship to the unicellular as to the multicellular forms.

[3] Flint's records of possible tetrasporangia in *Compsopogon* (1947) and *Kyliniella* (1953) are not included here. Their homology with tetrasporangia of the Florideophycidae seems doubtful, but without further information it is unwise to attempt an alternative interpretation.

TYPE I

FORMATION OF MONOSPORES FROM DIFFERENTIATED SPORANGIA

The cell division preceding formation of the sporangium differs from the vegetative divisions and results in the formation of a larger cell which remains sterile and a smaller cell which becomes the sporangium. The wall separating these two cells is often oblique and curved, and the contents of the two cells are often markedly different. The entire contents of the mother-cell are liberated as a monospore. Examples: *Erythrotrichia, Erythropeltis, Erythrocladia, Porphyropsis, Compsopogon, Kyliniella, Kneuckeria, Rhodochaete.* (Continued on page 561).

TYPE II

FORMATION OF MONOSPORES FROM UNDIFFERENTIATED VEGETATIVE CELLS

The last division preceding spore formation is in no way different from the usual vegetative divisions, i.e., a vegetative cell becomes a sporangium. The entire contents of the mother-cell are liberated as a monospore. Examples: *Porphyra, Bangia, Goniotrichum, Asterocytis, Neevea, Kyliniella, Porphyrella.* (Continued on page 564).

TYPE III

FORMATION OF A NUMBER OF SPORES BY SUCCESSIVE DIVISIONS OF A MOTHER-CELL

The cell divides by successive walls, more or less at right angles to those of the preceding division, during which process there is no great increase in the size of the mother-cell. A number of smaller cells, contained within the cell wall of the mother-cell, results, and a spore is formed from the entire contents of each of the smaller cells. Examples: *Porphyra, Bangia, Phragmonema, Cyanoderma*(?). (Continued on page 568).

In general, the spores of Types I and II have been considered to be asexual, but those of Type III have been variously interpreted. Those of *Porphyra* are considered by most writers to be carpospores resulting from fertilization of an egg-cell retained in the thallus. From a survey of the literature it appears that such spores of *Bangia* are sometimes considered asexual, at other times sexual

and hence as carpospores. In the genera *Phragmonema* and *Cyanoderma* they are regarded as asexual.

Apart from Dangeard's evidence (1931) that spores of both Type II and Type III may occur on the same thallus of *Porphyra leucosticta,* it is not clear whether spores of more than one type may occur on one thallus. While spores of Types II and III may occur in the same genus, those of Type I appear to be confined to certain genera, with the possible exception of *Kyliniella.*

No reproductive cells are known for *Goniotrichopsis* and *Bangiopsis.*

TYPE I

FORMATION OF MONOSPORES FROM DIFFERENTIATED SPORANGIA

(Continued from page 560)

While a vegetative cell assumes a reproductive function in spore formation in Types II and III, a sporangium is cut off from a vegetative cell in Type I. The formation of the sporangium is a distinctive process, and an oblique and curved wall laid down across a corner of the apical end of the cell separates the cell into two unequal portions. Such a wall appears only in connection with the formation of a sporangium, and the process may be repeated by the same cell several times. We are indebted to Thuret (*in* Le Jolis, 1863) for the first figure of this type of sporangium formation in an alga to which he gave the name *Erythrotrichia ceramicola.* Descriptions of the process were given later by Berthold (1882) for an alga to which he gave the same name as Thuret and for other species, in addition. Finally a fuller account has been given by Rosenvinge (1909, p. 68) for *E. carnea* as follows: " Its formation (i.e., the sporangium) begins with the nucleus dividing into two, the one lying over the other at the one side of the cell. Then the chromatophore divides longitudinally into two of unequal size lying side by side; the larger later moves upwards and is taken up in the spore together with the upper nucleus. In the lower chromatophore the pyrenoid is very small and indistinct shortly after the division, while the upper contains a large and distinct pyrenoid; it is therefore probable that the original pyrenoid passes over into the larger chromatophore, while a new pyrenoid is formed in the smaller. The fructiferous cells contain many

small starch grains which stain dark violet with iodine; they are to be found in the sporangia as well as in their sister-cells. The sporangium is in general smaller than its sister-cell; when the mother-cell is very short, however, they can be of equal size or even larger. As shown by Thuret and Berthold, the underlying cell, after the evacuation of the spore, expands and occupies the place of the original mother-cell, the process of spore-formation may be repeated". (Cf. Pl. I, C.)

In those species in which the erect filaments develop from a disc, such as *E. japonica* (Tanaka, 1952), *E. tristanensis* (Baardseth, 1941) and *E. polymorpha* (Howe, 1914), spores may be formed from the cells of the disc as well as from those of the erect filaments.

In his diagnosis of the genus *Erythropeltis,* Schmitz (1896, p. 313) states that asexual reproduction is similar to that of *Erythrotrichia*; this was confirmed by Batters (1900, p. 376) when he described a var. *Flustrae* of *E. discigera.* However, Dangeard[4] (1932) notes that the wall which cuts off the sporangium is not oblique in *E. discigera* (which he refers to under the older name *Erythrotrichia discigera*) but that the sister-cell of the sporangium occupies the cavity left after liberation of the spore from the sporangium.

Information about reproduction in the genus *Erythrocladia,* in which the thallus consists of a small disc of creeping filaments, is very scanty. Rosenvinge (1909), in describing the genus, states that the monosporangia are formed in the same way is in *Erythrotrichia.* However, it appears doubtful that this is true of *E. polymorpha* described by Dangeard (1932), for whole portions of the disc are to be found without cell contents and other cells in the spore-producing regions may be undivided or divided into two equal or unequal cells. It is possible that this species is not a true member of the genus *Erythrocladia.*

Rosenvinge (1909) found that the type of spore formation characteristic of *Erythrotrichia* occurs also in the alga known at that time as *Porphyra coccinea,* and he considered this character to be

[4] This same investigator (1949) also notes that spore formation in *E. Welwitschii* resembles that of *Bangia,* not that of *Erythrotrichia,* as each cell in the apical part of the filament liberates the entire contents as a single spore.

of sufficient importance to warrant removal of this species to a separate genus, to which he gave the name *Porphyropsis*.

The so-called macroaplanospores of the genus *Compsopogon* are formed in the same way as the monospores of *Erythrotrichia*, their formation having been clearly described by Thaxter (1900), (Pl. I, H), Brühl and Biswas (1923; 1927), Krishnamurthy (1953) and Jones (1955). Details of formation of the microaplanosporangium in this genus are not available, the fullest accounts being given by Thaxter (1900) and Brühl and Biswas (1923, 1927). It may well be of the *Erythrotrichia* type, however.

In describing the little-known genus *Kneuckeria*, Schmidle (1905) states that the reproduction is as in the genus *Compsopogon*, and in the equally little-studied genus *Rhodochaete*, Bornet (1892) found that the sporangia develop in the same general manner as in *Erythrotrichia*. However, further study of both of these rarely seen genera is obviously desirable.

Finally, reference should be made to the genus *Kyliniella*. Whereas Skuja (1928) has described the liberation of the entire contents of an undifferentiated cell as a single spore, Flint (1953) describes and figures sporangia of the *Erythrotrichia* type for a species from the United States of America. In addition, he says that the protoplasts of some cells were " opaque and contorted, but appeared to have two or four segments ". Further information about spore formation in this genus is desirable.

Spores formed in sporangia of this type are liberated by a rupture of the sporangium wall, and both Berthold (1882, for *Erythrotrichia*) and Flint (1953, for *Kyliniella*) suggest that expulsion is comparatively energetic. Brühl and Biswas (1923) similarly record that the microaplanospores of *Compsopogon coeruleus* are expelled with a jerk and projected some distance. By contrast, the macroaplanospores of *Compsopogon* glide out of the sporangium (Brühl and Biswas, 1923, 1927; Krishnamurthy, 1953). These authors, as well as Thaxter (1900), record that the liberation of macroaplanospores takes place at night.

In contrast to spores of Types II and III, these spores do not appear to show amoeboid movement[5] or change of shape after

[5] Dangeard (1932, p. 147) reports amoeboid movement of the spores of *Erythrotrichia discigera* (= *Erythropeltis discigera*).

liberation. On the other hand, Rosenvinge (1927) has recorded what he calls "conspicuous gliding movements" by the released spores of *Erythrotrichia reflexa* and *E. carnea*. He believes that the type of movement displayed by these spores shows considerable resemblance to that of diatoms. Movement may, however, be combined with rotation of the vertical axis. The speed of movement is variable, the quickest recorded being 50 μ a minute for *E. reflexa* and 120 μ for *E. carnea*.

In some of the genera referred to in this section, germination of the spores has been observed. Chemin (1937) showed that the filaments resulting from such spores of *E. carnea* resemble those from which the spores are liberated. More recently, Krishnamurthy (1953) has observed the germination of macroaplanospores of *Compsopogon* sp. to give a disc of creeping filaments, from which the erect filaments then develop. They are similar to the filaments on which the spores are formed. As is to be expected, there are differences in the first stages of germination between those species of *Erythrotrichia* which possess a basal disc and those which do not. In the former, the first wall in the spore is at right angles to the substratum, but parallel to it in the latter. In the former, the two cells give rise to creeping filaments, but in the latter, the lower cell becomes rhizoidal, the upper only growing into an erect filament. Spores of *Erythrocladia* germinate as do those species of *Erythrotrichia* which possess a disc.

TYPE II

FORMATION OF MONOSPORES FROM UNDIFFERENTIATED VEGETATIVE CELLS

(Continued from page 560)

In some genera which have filamentous thalli and also in *Porphyra* the entire contents of certain undifferentiated cells of the thallus may be liberated as a monospore. The cell division preceding formation of the spore does not differ in any way from normal cell-division.

Formation of such spores is either rare in the genus *Porphyra* or has been consistently overlooked. Records[6] of the occurrence of spores called "monospores", "gonidia" or "neutral spores"

[6] Hus (1902, pp. 188, 189) referred to thick-walled cells among "sporocarps" as monospores, but states that he is not sure whether they have any reproductive function or not.

have been given by Kusakabe (1929) for *P. tenella,* Ueda (1929, 1937) for *P. tenera,* Dangeard (1931) for *P. leucosticta,* Kunieda (1939) for *P. tenera,* Rees (1940a) for *P. umbilicalis* and Tanaka (1952) for *P. Okamurai* and *P. yezoensis.* Owing to paucity of detail, it is not certain that all these records refer to the same type of spore formation. Dangeard (1931) states that the spores are formed at the margin of the thallus, and from the figure given (Fig. 5, L) and reproduced here as Pl. II, it is clear that they are monospores of the type under consideration. Tanaka, in a diagnosis of the genus *Porphyra,* states (l.c., p. 26): "asexual reproduction by monosporangia involving large continuous areas of the frond" and reports the occurrence of such in the two species mentioned above. In both, the asexual plants are minute compared with the sexual, and continuous bands of vegetative cells at the margin of the thallus are transformed into monosporangia, one cell becoming a monosporangium. The spores are liberated by general dissolution of the mucilage between the cells.

In February, 1950, I observed the liberation of the entire contents of marginal cells as monospores from four thalli of *P. umbilicalis* var. *laciniata,* collected in North Wales. Apart from the presence of ragged edges here and there, these thalli were indistinguishable from sterile thalli. The spores escaped through a hole in the cell wall, the process taking about 15 minutes in those watched. Comparatively thick-walled cells were found clinging to the edge of thalli, collected in September, 1954, and February, 1955, in Wales, but it is not known whether these were liberated monospores or detached vegetative cells.

Kusakabe (1929, p. 22) states that the monospores of *P. tenella* are liberated on the flood of the spring tides and that the first crop is set free in Japan in the autumn. This occurrence is related to the drop of the mean air temperature to 20° C. Injury to the frond also induces spore formation. Ueda (1929, pp. 140, 141) states that he found monospores being liberated from the marginal cells of very young fronds three to four millimeters in size in November, 1926. In the following July he collected very small thalli, and in culture at 15.5° C. monospores were liberated within 24 hours. Monospore formation was induced also at 17.4° C. and 20.5° C. but not at higher or lower temperatures. The method of formation of these monospores is not stated.

While the liberation of spores has been seen and recorded fre-

quently in *Bangia fuscopurpurea* (Cohn, 1867; Reinke, 1878; Berthold, 1882; Schmitz, 1897; Kylin, 1922; Dangeard, 1927; Drew, 1952) and also in *B. lutea* and *B. atropurpurea* var. *heteronema* (Derbès and Solier, 1856), *B. atropurpurea* (Reinke, 1878) and *B. pumila* (Darbishire, 1898), it is not clear whether the spores in question belong to Type II or Type III as designated in this article. This is due to the fact that the majority of the accounts refer to multiseriate filaments, and it is not known whether the divisions leading to the multiseriate condition are always vegetative. Similarly, it is not known whether multiseriate filaments may remain in a sterile condition for a certain period before forming reproductive cells. Filaments of *Bangia* are uniseriate when young, and Drew (1952, Fig. 2, E, Fig. 4, A) has described the liberation of the entire contents of the cells at the apex of such filaments as monospores (Pl. I, G). Schmitz (1897) and Kylin (1922) also mention liberation of monospores from uniseriate filaments. It is by no means rare when observing such young uniseriate filaments to find that a division parallel to the long axis of the filament may take place before spore formation, and then two monospores are liberated side by side (Drew, 1952, Fig. 2, F & G). A further division at right angles to the first may result in four spores being liberated from the same level. As the filaments become multiseriate and walls are formed at right angles to the long axis of the filament as well as parallel to it, the resulting cells become smaller and smaller, and smaller spores result (Darbishire (1898) records that 64 may be formed from one mother-cell). Whether there is any distinction between such spores and those referred to by the earlier writers as "carpospores" (Type III of this article) is not clear.

Other genera in which monospores appear to be formed from the entire contents of undifferentiated cells are *Goniotrichum, Asterocytis, Neevea, Kyliniella* and possibly *Porphyrella.*

In *Goniotrichum* the spores may be liberated from both the uni- and multi-seriate parts of the thallus, but in the latter case there is no decrease in the size of the cells or spores as in *Bangia.* The spores may be liberated at the apex of the filament by dissolution of the thick mucilaginous sheath (Berthold, 1882; Schmitz, 1894; Børgesen, 1927; Smith, 1943; Tanaka, 1952) or else laterally. Chemin (1937) states that, in the latter case, no trace is left of the passage of the spore through the mucilage.

Asterocytis ramosa, although filamentous in appearance, is not essentially different from colonial types and may exist in chroococcoid stages. The contents of the entire cell may be liberated as a single naked spore, a process first described by Schmitz (1894). In addition, there are thick-walled cells which have been called "akinetes"[7] (Wille, 1900; Rosenvinge, 1909; Howe, 1920; Børgesen, 1927; Tanaka, 1944; Waern, 1952).

In the original description of *Neevea*, Batters (1900) wrote "Reproduction effected by the escape of the cells from the gelatinous sheath and their subsequent development into new individuals?" From the figure the reader is left to infer that each cell liberates a single spore. However, in Newton (1931, Fig. 152, C) the figure suggests that each spore divides further into four or eight cells. Additional observations on this little-known alga are obviously needed.

Formation of spores in the European material of *Kyliniella latvica* has been observed, but rarely. The earlier material found by Skuja (1926) in Lettland, on which the original description of this genus was based, and also that studied by Geitler (1954) were both sterile. A subsequent collection of material by Skuja (1928) contained thalli which liberated monospore-like structures with a very thin wall after they had been brought into the laboratory. Each such spore was formed from the entire contents of a vegetative cell and was liberated through a lateral aperture in the mother-cell wall. This type of spore formation is fundamentally different from that described by Flint (1953) for the American material of *Kyliniella*.

The nature of the limiting layer of these monospores at the time of their release has not been clearly established. They are frequently said to be "naked", and this suggests that the limiting layer is very thin and non-rigid. This is clearly the condition in those spores which squeeze through an aperture in the mother-cell wall, e.g., *Porphyra umbilicalis* var. *laciniata*. Spores of *Bangia* and *Porphyra* are said to show amoeboid movement when released, but, since it is not clear whether the accounts refer to spores of Type II or Type III, this will be discussed in the next section.

[7] Use of the term "akinete" is justified by Wille (l.c.) and also by Rosenvinge (l.c.) in the fact that the outer layers of the wall of the spore are formed from the inner layers of the gelatinous wall of the filament. It is not stated whether such akinetes undergo a period of rest before germination, when they have been observed to grow directly into new filaments.

As regards the manner of germination of the spores under consideration, there is evidence in *Bangia* to show that spores formed in this manner, i.e., singly from the entire contents of an undifferentiated cell, germinate to give filaments similar to those from which they were formed (Drew, 1952). Although the method of their formation is not precisely stated, it has been demonstrated frequently that spores of *Bangia* germinate to give filaments similar to those from which the spores are released (Derbès and Solier, 1856, for *B. atropurpurea*; Cohn, 1867; Goebel, 1878; Berthold, 1882; Kylin, 1922, 1946; Hamel, 1924; Dangeard, 1927; Drew, 1952, for *B. fuscopurpurea*). Dangeard (1931) germinated spores of Type II of *Porphyra leucosticta* and watched them develop into a short row of quadrate cells attached to the substratum by a rhizoidal outgrowth of the basal cell. Had these germlings been grown further, it is likely they would have developed into leafy thalli. Kusakabe (1929) states that monospores of *P. tenella* germinate to give leafy thalli.

Similarly, Chemin (1937) has shown that this type of spore of *Goniotrichum elegans* gives rise to a filament similar to the parent filament. Germination of such spores of *Kyliniella latvica* into discs has been observed by Skuja (1928). In all the cases mentioned, germination takes place soon after liberation without a period of rest.

It appears likely, therefore, that this type of spore formation is asexual and serves to repeat both the same somatic phase and also the same nuclear phase of the life history.

TYPE III

FORMATION OF A NUMBER OF SPORES BY SUCCESSIVE DIVISIONS OF A MOTHER-CELL

(Continued from page 560)

Formation of spores by successive divisions of a mother-cell by walls laid down in two or three planes at right angles to each other, without much enlargement meanwhile of the original cell, has long been known in *Porphyra* and alleged in *Bangia*.

Spore formation of this type occurs also in the filamentous genus *Phragmonema*, the only species, *P. sordida*, having been described by Zopf (1882), who found it growing on *Ficus barbata* in the

orchid house of the Botanical Garden in Berlin. Zopf (l.c., p. 49) noted that after a period of vegetative division the cells of the uniseriate filament divided by endogenous walls which were alternately longitudinal and transverse to give eight daughter-cells or even more in wider filaments (Pl. I, F). He called the resulting spores "coccen". Their formation might start either at the apex or in one or several intercalary positions, and they were to be found in large numbers. On tearing a filament, they might escape, but the normal method of liberation is dissolution of the mucilage. Liberation can be easily delayed or stopped altogether. If spores remain in the mucilage, it appears that a so-called zoogloea-stage develops, but if they become free, they lie either singly or in groups and undergo cell-division. Zopf failed to trace the further development of these spores but believed he had some evidence in support of the view that filaments develop from the zoogloea-stage. Geitler (1924) records the occurrence of this alga in a warm-house in Vienna and also (1942–3) in two out-of-door localities in Austria. In the latter collections, it existed in a reduced form consisting of short, few-celled, filaments growing so close together that a pseudo-parenchymatous structure resulted. The filaments disintegrated easily into single cells or few-celled fragments and might then divide irregularly. Geitler (1942–3) also reports that among unicells he saw not only the cell-contents slip out of some cells but also the formation of two or four autospores in a cell. The formation of these autospores resembles that of autospores described by the same author for the unicellular alga *Rhodospora sordida* (Geitler, 1927). In the earlier paper (1924) Geitler figured a six-celled filamentous germling of *P. sordida* from the warm-house material.

In the rarely studied genus *Cyanoderma,* Weber Van Bosse (1887) found that any cell of *C. bradypodis,* an alga inhabiting the hairs of the sloth, might become a sporangium. By repeated endogenous divisions, a variable number of reproductive cells could be formed, as many as 40 developing in one mother-cell. These "conidia", as she called them, were three to four μ in diameter and were liberated by dissolution of a part of the cell-wall. Germination of these spores was not seen, although young stages in the development of the thallus were present in the material. Recently, Bourrelly (1954) has confirmed these observations on living material and suggests a relationship to *Phragmonema.* A detailed

investigation would show whether the spores described are homologous with those of *Phragmonema,* on the one hand, and with *Porphyra* and *Bangia,* on the other.

The most frequently occurring spores in the genus *Porphyra* are those which are formed by successive divisions of mother-cells, the volume of those cells increasing little and their original walls remaining distinct meanwhile. Every cell in large areas of the thallus are often concerned in this type of spore formation. In surface view "packets" of spores are to be seen retained within the wall of the mother-cell in the mature condition, and these are liberated by subsequent dissolution of these walls and the intervening mucilage. Pl. I, K, shows stages in the development of, as well as mature "packets" of, such spores as seen in transverse section of a thallus of *P. umbilicalis* v. *laciniata.* Accounts of such spore formation are given by Nägeli (1847) for *P. vulgaris*[8], Janczewski (1873) for *P. leucosticta* and *P. laciniata,* Thuret and Bornet (1878) for *P. laciniata,* Berthold (1882) for *P. leucosticta* and *P. laciniata,* Dangeard (1927) for *P. linearis* and Kunieda (1939) for *P. tenera.* In addition, Hus (1902) described the formation of such spores in detail for a number of species on the Pacific Coast of North America.

There is lack of agreement regarding the position of the first walls in the division of the mother-cells leading to the formation of these spores. At the same time, great emphasis has been laid on this character in connection with the interpretation of these spores. Nägeli, Janczewski, Thuret and Bornet, Berthold and Dangeard all consider the first wall in the cell regarded as a mother-cell, to be parallel to the surface of the thallus. On the other hand, Hus, who followed the formation of these spores in detail in 11 species, found that the first wall is at right angles to the surface of the thallus and that, with one exception, the next wall in each of the daughter-cells, while at right angles to the first, is also at right angles to the surface, thus giving a cruciate pattern as seen on the surface. In the exception (*P. amplissima*) the second walls may be either parallel to the surface or at right angles to it. The wall formed in each of the four segments is parallel to the surface, thus resulting in eight daughter-cells, and in many species the process

[8] The binomials quoted are those used by the authors referred to, without implying that the identification is correct.

stops at that stage. In others, however, a further cruciate division takes place in each segment, thus bringing the final number to 32. Each of the final segments forms a spore. The other writers listed consider that the usual number of spores is eight. Hus (1902) distinguishes between a vegetative division and a division in a mother-cell by the thickness of the wall and whether it undergoes dissolution at the time of the liberation of the spores. The other writers fail to state at exactly what stage they recognize a cell as a mother-cell, and this may well explain the different views. In addition, there is some variation in the thickness of the walls formed, leading to difficulty in distinguishing vegetative divisions from those of mother-cells on the basis of the distinction made by Hus (1902). It is to be noted that Hus states that the only divisions which occur in *P. miniata* v. *cunieformis, P. tenuissima, P. abysicola* and in some instances in *P. amplissima* are the first two, leading to the formation of four segments arranged in a cruciate manner, both walls being at right angles to the surface of the thallus. While Hus maintains that such spores are homologous with those in which there is further division of the four segments by a wall parallel to the surface, Berthold and his followers would probably not accept this view. In fact, Berthold (1882) describes the formation of asexual spores in just this manner and considers they are totally distinct from those in which division parallel to the surface of the thallus occurs. Hamel (1924) and Kylin (1946) hold the same view.

If Hus' interpretation regarding the position of the first wall is correct, there would appear to be no fundamental difference between these spores of *Porphyra* and those formed in the filaments of *Phragmonema* regarding the method of their formation. Hus (1902) was unable to find any evidence for considering the mother-cell, from which spores of this type develop, as a zygote. On the other hand, Berthold (1882) held that the mother-cell functions as a female gamete and is fertilized. In consequence the spores which develop from it are considered by him as carpospores, and this interpretation has been generally accepted. A few investigators (Derbès and Solier, 1856; Koschtsug, 1874; Knox, 1926) have maintained that these " spores " are female gametes. These divergent views will be considered more fully in the section dealing with the records of sexual reproduction in these algae.

Still less precise information is available about the occurrence of similar spores in the genus *Bangia*. While spores of Type II may develop from cells of both uni- and multi-seriate filaments, it has not been clearly established that this type of spore, namely Type III, may develop in both uniseriate and multiseriate filaments, although from a consideration of the existing literature this appears possible. In neither case has the development of such spores been followed in detail, however. Hamel (1924, p. 444) states that cells of multiseriate filaments may divide to give four or eight spores. In the formation of eight spores, a wall parallel to the surface of the thallus is formed, but no such wall occurs when four spores only result. By analogy with Berthold's (1882) work on *Porphyra*, the former appear to be carpospores, the latter asexual spores. On the other hand, Reinke (1878) suggested that fertilization of liberated cells might take place in *Bangia*.

Since some cells of a single filament of *Bangia* may form four spores and other cells of the same filaments divide to give eight, it has not been found easy to distinguish them. Further confusion has resulted from the development of spores of Type II on the same filaments as these spores.

The nature of the limiting layer of the newly liberated spores of this type appears to be in doubt. In *Porphyra* and *Bangia* some spores are round when liberated, but others are irregular and show amoeboid movement, suggesting that the limiting layer is exceedingly thin and non-rigid and not in the nature of a wall. Amoeboid movement has been described for spores of *Porphyra* and *Bangia* which are referred to in this review as Types II and III, although not so differentiated by the observers. In *Bangia*, most, if not all, of the observations appear to refer to spores of Type II, and in *Porphyra* to Type III. Accounts relating to *Porphyra* are given by Janczewski (1873), Goebel (1878), Berthold (1882), Joffé (1896) and Dangeard (1927); and to *Bangia* by Reinke (1878), Goebel (1878), Berthold (1882), Kylin (1922) and Dangeard (1927). It is not generally recognised that this so-called amoeboid movement results in little if any locomotion, although Kunieda (1939) states that such spores of *P. tenera* creep about. All other observers describe the process as one of continuous change of shape, the protoplast pushing out protuberances. Such protuberances may be broad and contain an arm of the chromatophore, but

others may be exceedingly fine. It is stated that spores may remain in this condition for a considerable time, 24 hours being quoted by Kylin (1922) and Dangeard (1927), 48 hours by Berthold (1882). Spores which have shown amoeboid movement have been known to grow into a thallus like the parent, but others have been known to develop into filaments of the *Conchocelis*-phase.

This amoeboid movement of the spores of Types II and III is thus very different from the movement of certain spores of Type I, described already. It is also different from the movement of liberated cells of *Asterocytis smaragdina* (Rosenberg, 1935) which resembles that of the vegetative cells of *Chroothece*.

As has been pointed out, in the genera *Porphyra* and *Bangia* some investigators have seen a distinction between those spores during the formation of which a wall parallel to the surface of the thallus occurs, and those in which no such wall is formed. Since both may occur on the same thallus, the difficulty of isolating such spores without the help of modern techniques has been considerable. However, Berthold (1882) and Kylin (1946) both maintain that they obtained evidence in certain species of *Porphyra* which led them to conclude that spores, during the formation of which no wall parallel to the surface occurred and considered by them as asexual, germinate to give "leafy "thalli. They similarly conclude that spores formed from a mother-cell, in which the first wall is parallel to the surface of the thallus, germinate into procumbent filaments. Subsequently, Drew (1949, 1954a) has demonstrated that these filaments give the *Conchocelis*-phase.

Beyond the fact that spores liberated from multiseriate filaments of *Bangia fuscopurpurea* may germinate to give either a filament similar to the parent or, very much more rarely, a phase corresponding to the *Conchocelis*-phase of *Porphyra,* no connection between the manner of germination of the spore and its method of formation has been established.

The *Conchocelis*-Phase of *Porphyra* and *Bangia*

It has long been known that the spores of species of *Porphyra* formed by repeated division of a mother-cell germinate into fine, irregular, procumbent, filamentous growths. This has been demonstrated for *P. laciniata* (Janczewski, 1873; Thuret and Bornet,

1878; Kylin, 1922, 1946), *P. leucosticta* (Janczewski, 1873; Dangeard, 1931; Kylin, 1946), *Porphyra* sp. (Yendo, 1919), *P. tenera* (Okamura, Onda and Higashi, 1920; Kunieda, 1939) and *P. umbilicalis* (Grubb, 1924; Dangeard, 1931). These observations were based entirely on cultures; identical creeping filaments have not been recorded as occurring in the sea[9]. No convincing evidence is available of the formation of reproductive organs on these creeping filaments grown in culture, although, on the basis of single examples, both Kylin (1922) and Grubb (1924) thought that monospores might be formed. Dangeard (1931, 1954), on the other hand, considered such growths protonemal, the "leafy" thalli arising on them as "pluricellular" buds, usually from the original spore. Kunieda (1939) looked upon the filamentous growths as pathological, and stated that such spores liberated into the sea pass into a resting state, in which they remain for several months. Drew (1949, 1954a) has, however, demonstrated that when such spores of *P. umbilicalis* var. *laciniata*, or the filamentous growths from them, are brought into contact with shell, the germ-tubes or filaments penetrate the shell matrix and develop into growths which were described by Batters (1892) as *Conchocelis rosea*. This is also true for *P. linearis* and an unnamed species of *Porphyra* (Drew, 1954a, p. 208) on the coasts of the British Isles. In addition, Kurogi (1953a) has confirmed the existence of a *Conchocelis*-phase for *P. tenera*, *P. sub-orbiculata*, *P. pseudo-linearis* and *P. umbilicalis* prox., and Graves (1955) for *P. capensis*. Drew (in Drew and Richards, 1953) has obtained the comparable phase for *Bangia fuscopurpurea*, and Kurogi (1954) for *B. gloiopeltidicola* as well as *B. fuscopurpurea*.

Under the name of *C. rosea*, this phase has been described by Batters (1892), Rosenvinge (1931) and Drew (1954a). The last mentioned noted, in addition, the non-septate nature of the young growths as well as the frequency with which the filaments fuse inside the shell. She also confirmed the formation and described the development of the structures called "inflations" by Batters, and "fertile cell-rows" by Rosenvinge.

The "fertile cell-rows" of *P. umbilicalis* var. *laciniata* (Drew,

[9] Rees (1940a & b) describes some filamentous growths from the sea, but, as no illustrations are given, comparison is valueless. The essential link, showing the suggested connection with *Porphyra umbilicalis*, is not given either.

1954a) originate as irregularly shaped, contorted swellings on the vegetative filaments, usually as lateral branches but occasionally as the terminal portions of filaments. These swellings reach a considerable size and may branch before any transverse walls develop. At first the contents of these swollen cells are dense and homogenous, but with increasing age their colour deepens and becomes localised in definite plastids which develop at intervals along the central axes of the initials, which are usually branched at this stage. Ultimately, transverse walls develop but they are never so thick as the peripheral walls. The cells of the mature "fertile cell-rows" are rounded and slightly longer than broad. In material grown in culture, no indication was seen by Drew (1954a) of the rounding up of the contents of the "fertile cell-rows" to form spores, but this has been described for naturally occurring material (Batters, 1892; Rosenvinge, 1931; Jao, 1937; Drew and Richards, 1953). Rosenvinge (l.c.) and Jao (l.c.) figure such spores escaping laterally from the cells, although it is difficult to see how this can happen in a shell matrix. Drew and Richards (l.c.), on the other hand, found evidence of the breakdown of the transverse walls after formation of the spores (a feature figured by Rosenvinge also) and their subsequent movement along the resulting tube to the surface of the shell where they are presumably liberated. The fate of the spores formed on the *Conchocelis*-phase is in considerable doubt and is dealt with in the section concerning life-histories.

Reference has been made already to the occurrence recorded by Gayral (1952) of branched, septate filaments in a culture of *Chroothece rupestris*. She compares these filaments both in origin and structure with the germlings of *Porphyra* which can develop into the *Conchocelis*-phase. In the absence of illustrations of the filaments of *C. rupestris*, their degree of resemblance to the filaments of what is suggested is the corresponding phase in *Porphyra* cannot be judged. Should further work show them to be homologous, however, the fact would be of considerable significance.

Records of Sexual Reproduction

Evidence of sexual reproduction consists of recognition of male and female cells and of observation of their fusion. Records of sexual reproduction have been published for the genera *Composo-*

pogon, Kyliniella, Porphyra, Bangia, Porphyrella, Erythrotrichia, Erythropeltis and *Erythrocladia.* As the evidence given in the various accounts is both incomplete and conflicting, it will be necessary to consider them in detail to assess their value. However, it is difficult to understand the account given by Flint (1947) of sexual reproduction for *Compsopogon,* an account which also includes references to tetrasporangia and to what appears to be a "*Chantransia*"-stage. No attempt has been made in this survey, therefore, to incorporate the details given by Flint (l.c.), relating to *Compsopogon* and interested readers should consult the original account.

Since the description of sexual reproduction in *Kyliniella* by the same investigator (Flint, 1953, p. 79) is unique in some respects, the following quotations are given to record the salient points made by Flint. He considers that two types of sexual reproduction occur within the one species: "In the one type two adnate cells developed respectively into one male and one female structure. The male structure lost pigmentation and turgidity, extended as a process through the sheath and gave rise to an unpigmented spermatium. In the meantime the adjoining cell developed into a greatly enlarged female structure. The spermatium was released in proximity to an apparently sensitised region of the enlarged cell and fertilization took place. Immediately following fertilization the spermatium was observed within the female structure. The fertilized cell subsequently became further enlarged, opaque and filled with granular material". "In the second type of sexual reproduction the male and female structures developed from cells having no obvious or uniform positional relationship to each other. The male structure included an unpigmented spermatium which developed at either end or at both ends of a laterally elongated cell devoid of pigment and with greatly reduced turgor. The female structure was a greatly enlarged cell provided with a tubular projection which extended through the sheath. One or more of the spermatia extruded from the male structure became agglutinated to the terminal portion of the trichogyne. In some instances several spermatia were noted as adnate to the exterior of a fertilised female structure". Later stages in the development of the zygote were not followed. Some of the relevant figures published by Flint are reproduced on Pl. III, L, M, O, P, Q.

The remaining genera for which sexual reproduction has been reported can be classified into two groups, the first containing *Porphyra, Bangia* and *Porphyrella,* the second *Erythrotrichia, Erythropeltis* and *Erythrocladia.* The spermatia of the first group occur commonly and are formed in the same way as the spores of the third type designated in this paper, i.e., several from one mother-cell (Pl. I, A). There is lack of agreement regarding the female gametes and the manner of fertilization. On the other hand, in the second group a fundamentally different type of spermatangium is reported; it is described as developing in the same manner as a monosporangium of the first type of spore designated, and each spermatangium releases a single spermatium (Pl. I, B & Pl. III, R). Fertilization of an unreleased female cell is described, but there is little evidence regarding post-fertilization developments. In fact, these events appear to have been observed exceedingly rarely.

It seems surprising that, within the single Order of the Bangiales, there should be two such fundamentally different types of spermatangium formation.

GENERA IN WHICH THE SPERMATIA ARE FORMED BY REPEATED DIVISION OF A MOTHER-CELL

Thalli of *Porphyra* are to be found having pale yellowish or greenish areas either along the margin (*P. umbilicalis* var. *laciniata*) or scattered irregularly over the thallus (*P. leucosticta*). These areas are made up of cells which have divided endogenously into a number of very small segments. The content of each segment forms a single body which is usually regarded as a spermatium and which is liberated by dissolution of the mucilaginous walls. The formation of these spermatia is similar in all essentials to that of the third type of spore described in the earlier section. Accounts are provided by Derbès and Solier (1856), Nägeli (1847), Janczewski (1873), Thuret and Bornet (1878), Berthold (1882), Hus (1902), Isikawa (1921), Grubb (1924), Dangeard (1927), Kunieda (1939) and Tanaka (1952). Tanaka (l.c.) considers that the first two divisions of the mother-cell are at right angles to the surface of the thallus, but all other writers regard the first division of the mother-cell as parallel to the surface of the thallus. In many species further divisions, both cruciate and

parallel to the surface of the thallus, result in the formation of 64 to 128 spermatia per mother-cell. In certain distromatic species, Hus (1902) states that only eight or 16 spermatia are formed.

As division of the mother-cell proceeds, pigment is lost by the plastid, but this process may proceed at different rates in the same species. The plastid also becomes considerably reduced in size but is recognisable in the liberated cell. The cells are liberated by dissolution of the mucilage of the walls and are usually reported to be non-motile. In accounts by early investigators (Derbès and Solier, l.c.; Koschtsug, 1874) reference is made to motility of the male cells, but these reports are usually considered erroneous and the results of contamination by another organism. Amoeboid movement of the spermatia in *P. tenera* is referred to by Kunieda (1939, p. 389).

Berthold (1882, p. 12) noted cells intermediate between spermatia and what he called "neutral spores", and Janczewski (1873, pp. 245, 250) claimed that the same mother-cell in both *P. leucosticta* and *P. laciniata* could give rise to both spores and spermatia.

Recognition of the female cells of *Porphyra* has been much more difficult and has depended on observation of the attachment of cells, considered to be spermatia, to them. A survey of the accounts shows considerable lack of uniformity, as can be seen by inspection of Pl. II, in which illustrations from various workers have been collected.

Some of the earlier workers (Derbès and Solier, 1856; Koschtsug, 1874) thought that fertilization took place between liberated spermatia and other liberated spore-like cells, and in more recent times this view has received some support from Knox (1926) studying *P. naiadum* in the Puget Sound region. The cells accepted as female gametes by Knox are formed in the same manner as the spermatia and would be included as spores under Type III of this review. Knox (1926) reports fertilization between liberated cells in *P. naiadum*, thus:

"The fusion of sperm and egg was observed in *P. naiadum*. Cells were found lodged one over the other; how long they had been in that position could not be determined. A passage was formed between the two (Fig. 29a). The contents of both were coarsely granular. Suddenly the contents of the upper one (sperm) started pouring into the other (egg) and in less than a minute the

fusion was complete. The passage was then narrowed and closed leaving the remains of the top cell, a hull with a few granules, lying on top of the frond (Fig. 29b). The fertilised egg rounded up noticeably. Further developments could not be determined, as the cells could be kept alive no longer under the microscope. Three or four cells were seen to fuse in this manner." Knox's figure 29 is reproduced as Pl. II, C.

In all other accounts of sexual reproduction in *Porphyra,* the female cell is described as remaining in the thallus and being fertilized in situ. As is apparent from the figures reproduced, there is far from uniformity among these accounts, namely those of Berthold (1882) for *P. leucosticta* and *P. laciniata,* Joffé (1896) for an unnamed species of *Porphyra,* Grubb (1924) for *P. umbilicalis,* Dangeard (1927) for *P. linearis* and *P. umbilicalis,* and Kunieda (1939) for *P. tenera.* While Berthold (l.c.) was of the opinion that normal carpogonia are of the same shape as vegetative cells (Pl. II, A), other observers state that the female cell has a protuberance of varying length which to them suggests a trichogyne (Joffé, 1896; Ishikawa, 1921; Dangeard, 1927; Kunieda, 1939) as illustrated in Pl. II, H, I, K, P. Berthold (1882) also observed cells with such protuberances and considered that they were old unfertilized carpogonia (Pl. II, D). However, Joffé states that they are to be found on young thalli, those on old thalli being of the same shape as vegetative cells. As Dangeard (1927) found that cells of *P. linearis* in the process of being fertilized never showed such protuberances (Pl. II, L), while those of *P. umbilicalis* did (Pl. II, P), he wonders whether this character may be of a specific nature. Even if this process is interpreted correctly as fertilization, it is still essential that the presence or absence of a trichogyne be clearly established in order that any comparison with the Florideophycidae shall have any value.

As to the distinguishing features of the female sexual cells before fertilization, Berthold (1882) states that in *P. leucosticta* they are larger and their colour is paler and less red. Kunieda (1939), on the other hand, states that the carpogonia of *P. tenera* become darker as they enlarge.

The details given by the various investigators of the fertilization process seem to vary according to whether the cell, recognised as the female gamete, has a protuberance or not. In those cases where

there is no such protuberance, a very fine tube [10] is said to grow from the spermatium, resting on the surface of the thallus, through the thick layer of mucilage to the protoplast of the female cell (Berthold, 1882; Joffé, 1896; Grubb, 1924; Dangeard, 1927), as illustrated in Pl. II, A, B, E, F, G & L. Several spermatia may make such contact with a single female cell. Joffé (1896) appears to have watched the contents of the spermatium pass into the female cell and says the process takes a quarter of an hour. In contrast, in those cases in which the female cell has a protuberance, the spermatium appears to be more or less engulfed by the female cell. Joffé (l.c.) does not describe the process but figures the spermatium partly inside the protuberance (Pl. II, H, I). Likewise, Kunieda (1939) did not see the fusion but gives figures showing the spermatium engulfed by the retracting protuberance (Pl. II, M, N, O). It is to be noted that there may be protuberances from both free surfaces of the female cell (Pl. II, K). Kunieda (1939, p. 389) considers that the "fertilization" of the first type is in reality parasitization by an Oomycete, found by him to be of common occurrence in the case of *P. tenera*. This interpretation receives support from the opinion that "fertilization" is more frequently observed after material has been in the laboratory for a few days. Hus (1902), who came upon no evidence of sexual reproduction while studying the species of *Porphyra* from the Pacific Coast of North America, also states that: "The outer jelly walls of nearly all the fronds examined were infested with bacteria, which formed narrow lines perpendicular to the surface of the frond, reminding one of the canals formed by the 'spermatia' at the time of fertilization of the 'procarps' as described by Berthold (1882). These canals were found in the jelly surrounding the vegetative and antheridial cells as well as surrounding the sporocarps". This reminds the reader of the recent description of a bacterium in the walls of *Kyliniella latvica* by Geitler (1954), although, as Hus gives no figures, it is not possible to judge whether the two are similar or not.

Cytological evidence in support of fertilization is limited to the observation of two nuclei in a cell by Joffé (1896) (Pl. II, E, G)

[10] Berthold (l.c.) states that this is seen more clearly by adding glycerine to living material, which treatment causes shrinkage of the protoplast and hence casts doubt on the interpretation.

and to two figures, one by Dangeard (1927, Fig. 12b), the other by Magne (1952, Fig. *d*). Dangeard's figure shows two adjacent cells, to one of which a fertilization canal is attached. In this cell a smaller and a larger nucleus are in contact, and in the neighbouring cell there is a single large nucleus, interpreted by Dangeard as a fusion-nucleus. Magne illustrates an elongated nucleus in prophase in a fine tube connecting a structure on the surface of the thallus with a cell of the thallus.

Since Berthold (1882) found walls, parallel to the surface of the thallus, in cells to which fertilization tubes were attached, such as have been described above, he concluded that such walls arose from the first division of the zygote, and later investigators have accepted this interpretation. Subsequently the two daughter-cells divide by cruciate divisions into groups of spores, in fact, the spores described as Type III. However, Hus (1902) found no evidence that such spores had their origin in a zygote, and others, as has been stated, do not agree that in the formation of these "packets" of spores the first wall is parallel to the surface of the thallus.

Sexual reproduction in *Bangia* has been less thoroughly studied than in *Porphyra*. The formation of minute colourless cells, referred to as "spermatia", by repeated division of a mother-cell, has been described by Derbès and Solier (1856), Reinke (1878) Berthold (1882), Darbishire (1898), Dangeard (1927) and Drew (1952). The formation of spermatia begins at the apex of the filament and resembles the process in *Porphyra* in all essentials (Pl. I, A). Identification of the female cells prior to fertilization does not appear to have been achieved. Although the actual process was not observed by him, Reinke (1878) thought that the liberated spermatia possibly fused with liberated spores formed in the same manner as the spermatia and thus the third type of spore designated. The reason for this suggestion was the occurrence of spores, each with a prolongation, to which was attached a body resembling a spermatium (Pl. III, D). Goebel (1878) suggested that such appearances can be brought about by the amoeboid movement of these spores and have nothing to do with fertilization. Other observers—Berthold (1882), Darbishire (1898), Rosenvinge (1909), Schiller (1925), Dangeard (1927)—have alleged that a cell retained in the filament is fertilized in situ. It is not

clear whether the female cells are in uniseriate or multiseriate filaments or both. If the more generally accepted account for *Porphyra* be correct, they might be expected to occur in uniseriate filaments. Berthold (1882) seems to suggest their occurrence in uniseriate filaments, and the figures given by Darbishire (1898) for *B. pumila* and Tanaka (1944) for *B. yamadai* suggest this also. Dangeard figures multiseriate filaments of *B. fuscopurpurea,* the cells of which he considers are being fertilized, and so does Schiller (1925). It would appear that investigators have experienced difficulty in recognising the female gametes of *Bangia,* depending either on the attachment of what appears to be spermatia (Dangeard, 1927) or the method of germination of the resulting spores (Kylin, 1946). In no instance is it suggested that there is any prolongation of the female cell as a trichogyne as in *Porphyra,* and, Schiller excepted, the other writers follow Berthold in supposing that contact between the male and female gamete is established by means of a fine canal which grows from the spermatium, the body of which remains on the outside of the thallus (Pl. III, A, B, C, E, F, H). In Darbishire's (1898) figure of *B. pumila* the fertilization canal, as it is called, is still visible even after the cell has divided and appears to be in contact with one of the daughter-cells (Pl. III, H). This is comparable to a figure of Dangeard (Pl. III, F), in which a cell is shown containing two protoplasts, to each of which a spermatium is attached. Schiller (1925, Fig. 12, *3* and *4*), while not describing fertilization, figures the spermatium adpressed to the protoplast of the female cell and within the wall (Pl. III, G).

Cytological evidence of fertilization is given by Dangeard (1927, Fig. 3c and Pl. VIII, Figs. 1 and 3) who provides an illustration of what he considers to be the male and female nuclei in contact. Dangeard's Pl. VIII, Fig. 3 is here reproduced as Pl. III, E. The nucleus, accepted as the male (Pl. VIII, Figs. 1 and 3), has a prominent nucleolus and no chromatin, whereas at the time of liberation of the spermatium the nucleus is without a nucleolus and is in late prophase.

The zygote of *Bangia* is said to divide after fertilization to give a number of spores, usually eight but sometimes 16. Berthold (1882) considered the first wall to be periclinal, but Dangeard (1927) says it is anticlinal. A figure by Darbishire (1898) for *B. pumila* and another by Tanaka (1952) for *B. yamadai* suggest

no such regularity; instead of division of the zygote into cells, the contents of each forming a single spore, the protoplast appears to divide into spores direct (Pl. III, H).

In *Porphyrella,* a genus closely related to *Porphyra,* the spermatia seem to develop in the same way as described for *Porphyra.* Smith and Hollenberg (1943, p. 215) state that carpogonia are produced near the thallus margin by " a cell division in which there is a curving wall, quite similar to the curving walls producing the monospores of *Erythrotrichia,* and the cells thus formed are liberated singly. However it is uncertain whether the liberated cells are carpogonia or zygotes. In addition to this uncertainty concerning the time of fertilization there is nothing to indicate whether a liberated cell (zygote?) functions as a carpospore or divides to form a number of carpospores, each capable of developing into a new thallus ". Another explanation of these observations is that the liberated cells were in fact spores of the first type designated in this review, a resemblance noted by Smith and Hollenberg, and that the female cells were not seen. If the cell cut off by a curving wall in *Porphyrella* is indeed the female gamete, this genus would show affinity with both groups of genera recognized in this section; with the first by the manner of development of the spermatia, with the second by the resemblance between the manner of formation of the female gamete and of the monospores of *Erythrotrichia.*

GENERA IN WHICH THE SPERMATIA ARE FORMED SINGLY IN ISOLATED SPERMATANGIA

The development of a single spermatium in an isolated spermatangium in the same way as monospores are formed (Type I) has been reported in *Erythrotrichia, Erythropeltis* and *Erythrocladia,* genera usually placed in the Erythropeltidaceae, a family of the Bangiales. It has been pointed out that the Bangiaceae, a family in which the spermatia arise by repeated division of a mother-cell, as has just been described, belongs to this same Order.

The records of sexual reproduction for *Erythrotrichia, Erythropeltis* and *Erythrocladia* are both very few in number and very incomplete. General statements are not possible, therefore, and the only way of presenting the information available is to paraphrase or quote the statements in the original accounts.

In the genus *Erythrotrichia* the available information is mostly

confined to that published by Berthold in 1881 and 1882. The details he gives in the earlier paper are few and concern an unnamed alga. The second paper contains details for *Erythropeltis discigera* (Berthold) Schmitz (= *Erythrotrichia discigera* Berthold) and *Erythrotrichia obscura;* in addition, Berthold (1882) states that he saw spermatia on filaments of *Erythrotrichia ciliaris.* While the spermatia are formed in exactly the same way as the monospores of these species and, like them, have the power of gliding movement, they are smaller. On the other hand, they are larger than the spermatia of the *Bangia-Porphyra* type and, unlike them, contain an easily recognisable and pigmented chromatophore. Spermatia may be formed on special filaments or on filaments bearing either monosporangia or female cells in addition. The latter cannot be distinguished from vegetative cells before fertilization, but Berthold reported that a male cell becomes attached to a cell in a filament and that the two cells move together and fuse. Berthold is uncertain whether the resulting zygote divides into two cells or not. The figures appear convincing (Pl. III, N, R, S), but there is no evidence that the sequence suggested by him was definitely proven; in other words, it was not determined whether the small cell on the outside of the filament was establishing or losing contact. The occurrence of either two sizes of sporangium or of sporangium and spermatangium, the interpretation of the investigator, have been reported for another species of the genus *Erythrotrichia, E. tristanensis,* by Baardseth (1941). The smaller ones are confined to the erect branches of the thallus, but the larger ones develop on both the erect branches and the disc. Other references to sexual reproduction in the genus *Erythrotrichia* are rare and include that of Gardner (1927) for *E. Parksii* v. *minor.* This investigator expresses doubts, however, about his being the correct interpretation. To use Gardner's own words, he found certain cells in some filaments with " protoplasmic prolongations extending beyond the surface of the original cell walls at times, having attached small cells, seemingly the male gametes ". Formation of the attached cells was not observed, but monosporangia are shown on the filament figured.

When describing *E. reflexa,* Tanaka (1944, p. 89) states: " The carpogonia often produce a hyaline protuberance on the surface of the frond. The fertilized carpogonia divide a few carpospores (?) ". In the relevant figure (10B) (reproduced as Pl. III, I)

it is noticeable that some of the carpogonia are twice as big as others and appear to have resulted from divisions similar to those which give the spores. Spores are figured (l.c. 10C.) in multiseriate filaments (reproduced as Pl. III, K.). In a later paper, Tanaka (1952) states, with reference to a figure (10D) of *E. parietalis:* " A part of a female filament with fertilization tubes ". There is no mention of spermatia or evidence of such attached to the filament with the supposed carpogonia.

These quotations have been given to show the inadequacy of the evidence provided for statements which have considerable importance in an understanding of this group of algae. This applies with even greater cogency to the related genus *Erythrocladia,* for which the only references to sexual reproduction are those in a paper by Howe and Hoyt (1916) [11] for *E. recondita* and *E. vagabonda.* No details are given of the development of the sexual cells. In the diagnosis of *E. recondita* these writers state (p. 112): " spermatia ovoid, 2–4 μ in diameter, exerted or sub-exerted by slender stalks about 1 μ broad; carpogonia furnished with a beak or trichogyne exerted about 4–8 μ; sporocarps forming a single carpospore (or rarely 2), these ovoid, oblong, or irregular, mostly 8–19 μ in maximum diameter; non-sexual spores unknown ". In *E. vagabonda* comparable details are given in the diagnosis (p. 115). The authors state, however, that, though they have not been able to demonstrate sexuality so satisfactorily in this species, they do not doubt its existence: " In two instances we have seen a supposed spermatium resting on the general surface above a supposed carpogonium. We have not observed any carpogonium beak or trichogyne and think it must only be slightly developed, if present at all ".

It is clear that there is great need for a thorough investigation of these algae of the Erythropeltidaceae, particularly with regard to sexual reproduction.

LIFE-HISTORIES OF PORPHYRA AND BANGIA

In view of the lack of factual information, particularly regarding sexual reproduction, as well as the uncertainty concerning the interpretation of some of the recorded observations, any general

[11] Laing's (1928) account of sexual reproduction in *Erythrocladia* (?) *insignis* is both difficult to follow and open to serious question. The original should be consulted if necessary.

statements about the life-histories of these algae not only would be of no value but might easily be misleading. Some comments may be of help, however, and will be expressed in terms of the general concept of life-histories put forward by me elsewhere (Drew, 1954c, 1955).

This concept maintains a distinction between the life-history and the sexual cycle, and, on the basis of the available information, the life-history of many of the Bangiophycidae has no sexual cycle. It consists of the repetition of a single somatic phase either by means of vegetative cell division or by means of asexual spores, and very little is known about the cytology of these forms. On the other hand, sexual reproduction has been described for certain genera of the Bangiales, Goniotrichales and Compsopogonales. The available information is so scanty respecting all the genera concerned, except *Bangia* and *Porphyra,* that consideration will be limited to these two only. The following facts can be regarded as having been established in respect to the sequence of somatic phases in these genera:—

(1) Spores of Type II, i.e., formed singly from the entire contents of a cell resembling a vegetative cell, germinate to give thalli, morphologically similar to the one from which the spores are liberated, that is, the same somatic phase. This is well established for *Bangia,* but, while it is assumed by many writers, the only experimental evidence that this happens in *Porphyra* is that of Dangeard (1927) for *P. leucosticta.* Development of the germlings beyond the first stages of a very few cells was not followed.

(2) Spores of Type III, i.e., formed by repeated division of a mother-cell and giving more than four spores, germinate to give the *Conchocelis*-phase. This is a phase morphologically different from the one from which the spores are liberated, i.e., a second somatic phase [12]. This sequence is well established for *Porphyra,* but it cannot be said that the method of formation of the spores

[12] Rees (1940b) describes the occurrence of "plantlets" in an account of the life-history of *P. umbilicalis.* These "plantlets" were free-living entities growing on concrete chippings attached to concrete walls in the sea. In another paper (1940a) these microscopic growths are said to be 4-14 cells long and to have two or three short branches. The cells measure 16.0-20.0 by 4.0-5.0 μ and spores liberated from them are 11.0-14.0 μ in diameter. These, he assumes, give rise to the leafy thalli of *P. umbilicalis,* but essential evidence showing the connection between the two is not given.

from which the *Conchocelis*-phase of *Bangia* develops has been followed critically.

As has been pointed out, there is doubt that the spores from which the *Conchocelis*-phase of *Porphyra* develops are carpospores. The general view is that they are carpospores, but, even if this is correct, there is conflicting evidence about the chromosome complement (Dangeard, 1927) maintaining that these spores of *Porphyra* are haploid and (Magne, 1952) that they are diploid. If they are zygotes, the *Conchocelis*-phase is likely to be diploid. However, if they are neither zygote nor carpospores, the change of somatic phase from the "leafy" thallus of *Porphyra* to the simple *Conchocelis*-phase may be correlated either with a change of nuclear phase or with physiological factors. Until more is known on these points, interpretation of the *Conchocelis*-phase is best left. Dangeard (1931, 1954) continues to uphold the view that it is protonemal and that the leafy thalli arise on it as "pluricellular buds", often from the original spore.

It is known that spores are formed on the *Conchocelis*-phase of *Porphyra,* the entire content of a single cell of the so-called "fertile cell-rows" being transformed into a spore. The development of the "fertile cell-rows" shows unique features, the significance of which is not yet understood (Batters, 1892; Rosenvinge, 1931; Drew, 1954a). For example, the "fertile cell-row" initial increases in size and branches before it is divided into cells by the formation of transverse walls.

The events following the maturation of the *Conchocelis*-phase with its fertile cell-rows are not known with certainty, and the following summaries of recent observations will indicate the present state of our knowledge about them:

(1) Kurogi (1953b) found that an abundance of spores appeared over a period of time on the bottom of three dishes, in each of which was suspended a shell infected with the *Conchocelis*-phase of *Porphyra* spp. On germination, these spores formed a short uniseriate row of cells, apart from those of *P. umbilicalis* prox., in which a longitudinal division took place in the apical cell at an early stage. Only very early stages were seen, and no germling figured has more than 15 cells. Kurogi concludes that the spores liberated from the *Conchocelis*-phase "germinated into such a bud of the leafy thallus of *Porphyra* as is found in the sea and did not

penetrate again into the shells". Kurogi (1954) considers the same to be true for *Bangia gloiopeltidicola*.

(2) Drew (1954a) has shown that "plantlets" of microscopic proportions, but consisting of 50–100 or more cells, develop in the interstices of shells or on the surface of shell flakes "infected" with the *Conchocelis*-phase of *P. umbilicalis* var. *laciniata*. These "plantlets" vary in shape from tufted filamentous growths to discs, pseudoparenchymatous in the centre with short filamentous projections around the periphery. While some of these "plantlets" were unattached in the cultures, others developed from an extension of a cell of a fertile cell-row of the *Conchocelis*-phase. Rarely did they appear to be attached to a filament similar to that of the *Conchocelis*-phase. No clear evidence of spore formation on these "plantlets" was obtained by Drew.

(3) Drew (1954b) has shown that sterile shells suspended in culture vessels containing shells "infected" with the *Conchocelis*-phase of *Porphyra umbilicalis* var. *laciniata* and others with the corresponding phase of *Bangia fuscopurpurea* may themselves become "infected". Whether this sub-infection is brought about by filaments or by spores is unknown.

(4) Graves (1955) has recently published a short account of her work on *P. capensis*, confirming the existence of a *Conchocelis*-phase. She has described also the formation of filamentous rows of sporangia, which are partly outside and partly inside the shell matrix in which the *Conchocelis*-phase develops. Each sporangium gives rise to a single spore, which may germinate before being liberated. The method of cell division in these germlings is similar to that observed by Kurogi (1953a) and suggests that they would develop into leafy thalli. Minute leafy thalli were found by Graves on the bottom of some of the culture vessels. Such spores, germlings and leafy thalli appeared after the *Conchocelis*-growths had been exposed to the air daily.

After seeing Drew's preparations, Graves believes that the rows of sporangia described by her resemble the more filamentous "plantlets" of Drew's cultures. The latter never formed any spores, however, but continued vegetative growth. Both Graves and Kurogi's cultures appear to have been kept at higher temperatures than Drew's and were possibly exposed to higher light intensities. Such differences, either coupled with others or by themselves, may explain the different results. The relationship of fertile

cell-rows inside the shell matrix to "plantlets" formed both in interstices in the shell and on the surface has still to be clarified. As a result of Kurogi and Graves' work, it appears likely that leafy thalli can develop from spores formed in growths originating from the *Conchocelis*-phase. The spread of the *Conchocelis*-phase from shell to shell (see (3) above) has still to be explained.

To sum up, the existence of the *Conchocelis*-phase in the life-history of *Porphyra* has been well established, and, while it appears likely that spores from growths originating from this phase can give rise to leafy thalli, details still await clarification. It would seem necessary also for the leafy thalli arising from these spores to be grown to maturity. Likewise, until the details of sexual reproduction have been clearly established and a thorough cytological examination completed, the course of the sexual cycle remains open to doubt.

The only information about the corresponding stage in the life-history of *Bangia* is provided by Kurogi (1954) who states that monospores are liberated from the "*Conchocelis*-thalli" of *B. gloiopeltidicola* and germinate into a "bud of *Bangia*-thallus".

In conclusion, brief notes summarising what is known about reproduction in each of the genera of the Bangiophycidae will now follow. Where the information depends on a few observations, relates to a single species or differs from the evidence in general, references to the original publication are given.

SUMMARY OF INFORMATION ABOUT REPRODUCTION

Unicellular Types

PORPHYRIDIUM (*P. cruentum*). Simultaneous division of the cell-contents into four, occasionally eight (Geitler, 1944), separate cells, the parent cell-wall taking part: occurrence of four and more daughter-cells within the mother-cell wall (Geitler, 1944; Kufferath, 1920); liberation of contents of cell as monospore (?) (Vischer, 1935); budding off of small portions of cell, regarded as a pathological phenomenon (Geitler, 1944).

VANHÖFFENIA. *V. antartica:* resting cells (Wille, 1924).

CHROOTHECE. *C. mobilis:* release of cell-contents as single body (Pascher and Petrova, 1931). *C. rupestris:* formation of groups of four cells, interpreted as carpospores, each cell germinating into

septate, branched filament, interpreted as protonema, on which new thallus originates (Gayral, 1952). *C. mobilis:* quadrates of similar or dissimilar cells; if the latter, one or two thick-walled, the remainder thin-walled, the authors suggesting the latter may be spermatia (Pascher and Petrova, 1931).

RHODOSPORA. *R. sordida:* formation of four, 16 or 32 walled daughter-cells within the mother-cell and interpreted as autospores by Geitler; resting-cells (Geitler, 1927, 1955).

RHODOSORUS. *R. marinus:* reproduction unknown.

Multicellular Types

ASTEROCYTIS. Spores of Type II; akinetes.

GONIOTRICHUM. Spores of Type II.

GONIOTRICHOPSIS. *G. sublittoralis:* reproduction unknown.

NEEVEA. *N. repens:* spores of Type II (Batters, 1900) and Type III (Newton, 1931)?

BANGIOPSIS. *B. subsimplex:* information too fragmentary to classify.

PHRAGMONEMA. *P. sordida:* spores of Type III (Zopf, 1882); escape of cell-contents and also formation of two to four autospores per mother-cell in coccoid-state (Geitler, 1942–3).

CYANODERMA. Spores of Type III.

KYLINIELLA. *K. latvica:* spores of Type I (Flint, 1953); spores of Type II (Skuja, 1928); sexual reproduction (for details see Flint, 1953).

KNEUCKERIA. *K. pulchra:* spores of Type I (Schmidle, 1905).

ERYTHROCLADIA. Spores of Type I. *E. polymorpha:* spores of Type II (Dangeard, 1932); sexual reproduction reported for *E. recondita, E. vagabonda:* spermatia formed singly, fertilization of cell in thallus, but post-fertilization developments uncertain (Howe and Hoyt, 1916).

ERYTHROTRICHIA. Spores of Type I. *E. welwitchii:* spores of Type II (Dangeard, 1949); sexual reproduction reported for *E. obscura,* spermatia formed singly, fertilization of a cell retained in

the thallus, post-fertilization developments uncertain (Berthold, 1882). Other fragmentary records (see text p. 00).

ERYTHROPELTIS. *E. discigera:* spores of Type I; sexual reproduction reported, spermatia formed singly, fertilization of a cell retained in the thallus, post-fertilization developments uncertain (Berthold 1882, sub. *Erythrotrichia discigera*).

PORPHYROPSIS. *P. coccinea:* spores of Type I (Rosenvinge, 1909).

BANGIA. Spores of Type II, from which filaments similar to the parent arise; sexual reproduction; numerous spermatia from each mother-cell; fertilization of cell in thallus described (Berthold, 1882; Darbishire, 1898; Rosenvinge, 1909; Schiller, 1925; Dangeard, 1927) but the possibility of fertilization of a liberated cell suggested by Reinke, 1878; those holding the former view report division of zygote into eight to 16 spores (Type III); four asexual spores per mother-cell (Hamel, 1924). *Conchocelis*-phase occurs in *B. fuscopurpurea* (Drew and Richards, 1953; Kurogi, 1954) and *B. gloiopeltidicola* (Kurogi, 1954); monospores of *Conchocelis*-phase germinating into a "bud of *Bangia*-thallus" (Kurogi, 1954).

PORPHYRA. Spores of Type II, from which thalli similar to the parent probably arise, but the only experimental evidence is that of Dangeard (1931) for *P. leucosticta*; four asexual spores per mother-cell (Berthold, 1882; Kylin, 1946); sexual reproduction; numerous spermatia arising from each mother-cell; fertilization of a cell retained in the thallus described (Berthold, 1882; Joffé, 1896; Grubb, 1924; Dangeard, 1927; Kunieda, 1939), also of a liberated cell in *P. naiadum* (Knox, 1926); those holding the former view report division of the zygote into a number of spores (Type III); spores of Type III develop into the *Conchocelis*-phase in *P. umbilicalis* v. *laciniata* (Drew, 1949, 1954a), *P. linearis* (Drew, 1954a), *P.* sp. (Drew, 1954a), *P. tenera* (Kurogi, 1953a), *P. sub-orbiculata* (Kurogi, 1953a), *P. pseudolinearis* (Kurogi, 1953a), *P. umbilicalis* prox. (Kurogi, 1953) and *P. capensis* (Graves, 1955); various indications regarding the next step in the sequence of somatic phases; (i) occurrence of "plantlets" described by Drew (1954a) as well as spread of *Conchocelis*-phase

from shell to shell through culture medium (Drew, 1954b); (ii) germination of spores, which appeared in culture medium in which shells infected by *Conchocelis*-phase were suspended into a "bud of the leafy thallus of *Porphyra*" described by Kurogi (1953b); (iii) conclusion by Graves (1955) that "although the evidence was not conclusive, it would seem reasonably certain, in view of the precautions taken, that the young leafy plants had arisen from the filamentous plants growing in the same culture"; (iv) suggestion by Dangeard (1931, 1954) that the leafy thallus arises as a "pluricellular bud" on the free-living *Conchocelis*-phase; and (v) description by Rees (1940a, b) of microscopic growths which he found in the sea and which he considers belong to *P. umbilicalis*, although no evidence of the connection is given.

PORPHYRELLA. *P. gardneri:* spores of Type II; sexual reproduction; numerous spermatia from each mother-cell; cell cut off by curving wall interpreted as carpogonium or carpospore by investigators (Smith and Hollenberg, 1943).

COMPSOPOGON. Spores of Type I; microaplanospores, the exact method of formation of which not known; sexual reproduction: tetrasporangia and a "*Chantransia*"-stage described by Flint (1947) for unnamed material of *Compsopogon*.

RHODOCHAETE. *R. pulchella:* spores of Type I (Bornet, 1892).

DISCUSSION

The aims of this review have been to assemble the published facts regarding reproduction in the Bangiophycidae, to indicate the extent of the evidence and to consider the interpretation given to these facts. It has been shown that our knowledge of even the grosser features of the reproductive processes is very imperfect, and in some instances the evidence is unsatisfactory. This is particularly true of the processes referred to as sexual and above all of the cytological aspects of these events. Renewed observations, which will need to be highly critical to be of value, are very necessary, and it seems reasonable to expect that fresh investigations will lead to reinterpretation of some of the observations already recorded.

Orderly arrangement of the published facts has not been easy to achieve, owing to the lack of precision in the published accounts as well as to the lack of uniformity in the terminology used. The

latter appears to be due in some instances to the investigator's uncertainty regarding the phylogenetic relationship of the alga he was investigating, and in other cases to shortage of material for study. In some genera, e.g., *Rhodosorus* and *Goniotrichopsis,* only sterile material has been examined. The final arrangement of the material adopted in this review should be accepted as a system of tabulating the information available and as a basis for further study, not as an expression of any fundamental distinctions or relationships. This applies particularly to the types of spores recognised in the multicellular forms. Among these forms the differentiated sporangium, from which a single spore is liberated (Type I), is restricted to certain genera, *Kyliniella* and *Porphyrella,* both of which are in need of further study, being possible exceptions. While this type of sporangium appears to differ fundamentally from those designated as Type II and Type III, it is not yet clear how fundamentally Type II and Type III differ from each other and whether intergrades between the two are not to be found. On the other hand, there may be two fundamentally different types of spore formation included under Type III, the one asexual in origin, the other sexual. Recognition of spore formation in the unicellular forms presents additional difficulties, and a brief résumé of the literature is all that has been attempted. This does suggest, however, that study of these forms might help in interpreting the multicellular forms.

As regards the extent of the evidence, an attempt has been made both throughout the text and in the summary of information under generic headings to differentiate between those events which appear to be of common occurrence and those reported but rarely. Thus it will have become clear to the reader that there is no genus of the Bangiophycidae where the evidence concerning all the reproductive processes is satisfactory and that even in genera such as *Porphyra* and *Bangia,* probably the most extensively studied, much remains to be elucidated. Provided an effort to distinguish the normal from the abnormal is continually made, and that the conditions under which they are grown are satisfactory, our knowledge of reproduction in these algae could be extended by a study of them in culture. In the present state of our knowledge, few generalisations about the reproduction of these Bangiophycidae are warranted.

It will have been clear from the preceding pages that lack of precise information regarding certain critical events makes reliable interpretation impossible at present. This is particularly true (*a*) of the distinction between normal cell-division and spore-formation in both unicellular and multi-cellular forms, and (*b*) of the events leading to the formation of spores of Type III.

With regard to the first of these points, namely, the difference between cell division and spore formation, the subdivision of a cell leading to the formation of a number of daughter-cells has been reported for genera, both uni- and multi-cellular, and the question whether the daughter-cells should be regarded as vegetative cells, sporangia or spores is of significance. If they are spores or sporangia, each containing a single spore, it is important to know at what stage the process ceases to be vegetative. Two criteria which have been used for settling this point in the unicellular forms are:

(*a*) whether the divisions are successive or simultaneous

(*b*) whether the wall of the mother-cell participates in the formation of the wall of the daughter-cell.

Simultaneous division of the mother-cell has been described very fully by Geitler (1944) for *Porphyridium cruentum*. In this species, furrows, which originate at the periphery of the cell, segment the protoplast as well as the plastid and pyrenoid into four, occasionally eight, daughter-cells. Geitler (1955) questions whether simultaneous division may not take place in *Rhodospora sordida* also on account of the tetrahedral arrangement of the four daughter-cells, but divisions are clearly successive when a larger number of daughter-cells is formed (Geitler, 1927, 1955). Two-celled stages occur and this supports successive division; hence the tetrahedral arrangement of four cells may have some other explanation. The resulting daughter-cells of *R. sordida* have their own walls while still surrounded by the membrane of the mother-cell, and hence Geitler (l.c.) considers them autospores. On the other hand, since the wall of the mother-cell takes part in the formation of the walls of the daughter-cells of *P. cruentum*, formed by simultaneous division, Geitler considers that they are not autospores. In this connection, Kufferath (1920, p. 51) states that in his cultures of *P. cruentum*, he could distinguish two types of division of a mother-cell into two. In the one, there is a straightforward divi-

sion into two separate cells, but in the other, two or more daughter-cells are formed within the cell-wall of the mother-cell and are liberated subsequently by rupture of the mother-cell-wall. Kufferath regards the first type as vegetative and the second as sporangial.

Whether significance should be attached, on the one hand, to successive as opposed to simultaneous divisions, on the other hand, to whether the wall of the mother-cell contributes to the wall of the daughter-cell or not, is uncertain in the present state of our knowledge. By analogy with the tetrasporangium of the Florideophycidae, it would appear that these features may not be of great importance. Simultaneous division of a mother-cell into several daughter-cells suggests a different physiological process from normal cell division. In successive divisions the important point to ascertain is when the physiological change from a vegetative cell-division to the formation of reproductive cells takes place, and on this point there is little or no information, either regarding the changes which can be observed in the cell directly, or indirectly by means of biochemical tests.

Little attention has been paid to the method of distinguishing normal cell-division from spore formation in the multicellular forms. Hus (1902, p. 00) was aware of this problem when he was studying spore formation (Type III of this review) in several species of *Porphyra,* and he concluded that all walls which undergo dissolution at the time of liberation of the spores belong to the reproductive phase. In *Rhodospora sordida* the difference which can be observed between vegetative cell-division and autospore formation is that successive divisions take place without intervening cell enlargement and dissolution of the outer portion of the mother-cell wall which envelops the daughter-cells. Essentially the same differences are recognisable between vegetative cell-division and the divisions which lead to the formation of spores of Type III in *Phragmonema, Porphyra* and possibly *Bangia,* although no precise account of their formation is available in this last-named genus. Therefore it seems legitimate to question whether there is any fundamental difference between autospore formation in *Rhodospora sordida* and the formation of spores of Type III in the named multicellular genera.

With regard to the spores of Type III of *Porphyra,* on the basis of his diagnosis mentioned above, Hus (1902) asserted that the

first and second walls to be formed in spore formation are at right angles to the surface of the thallus. On the other hand, Berthold (1882) considered that the first wall is parallel to the surface of the thallus. The difficulty of distinguishing between vegetative and reproductive cell divisions possibly accounts for the discrepancy between these statements.

The lack of precision in the descriptions of events leading to the formation of spores of Type III is largely responsible for the different interpretations put forward respecting them. Spores of Type III of *Porphyra* and *Bangia* have been interpreted by the majority of those who have investigated them as carpospores and by a few as female gametes. In *Porphyra* Hus (1902) found no evidence to support either of these views, the other possibility suggested being that they are purely asexual.

The evidence for considering these spores of *Porphyra* and *Bangia* as carpospores rests primarily on the evidence of fertilization of cells retained in the thallus. The available evidence for this has been fully set out, with the relevant illustrations, in this review. It has been pointed out that among those who look upon spores of Type III of *Porphyra* as carpospores, there is disagreement about the method of fertilization. Some believe that a fine tube grows out from the spermatium on the surface of the thallus, through the mucilage and into the cell considered the female gamete. Kunieda (1939, p. 389) suggests that this is possibly not fertilization at all but parasitization by an Oomycete. Hus (1902), as has been stated already, found bacteria in the mucilage of *Porphyra* resembling the "fertilization canals" of Berthold (1882). When writing of *Porphyra umbilicalis*, Rosenvinge (1909, p. 63) noticed that "fertilization canals" were abundant, and often several connecting to a single cell were to be seen. Yet, on another occasion, specimens which he identified as belonging to f. *linearis* and f. *laciniata* contained "cystocarps" but no trace of either spermatia or "fertilization canals".

In addition, both Janczewski (1873, p. 247) and Hamel (1924, p. 436) state that on occasions both spermatia and spores of Type III may develop from the same mother-cell [13]. This means either that both asexual and sexual spores may be formed in the same way or that spores, regarded by most investigators as carpospores,

[13] Berthold (1882, p. 13) refers to similar occurrences but interprets the spores as neutral spores.

are not formed from a zygote and therefore are not to be regarded as carpospores. These spores, that is Type III formed from repeated division of a mother-cell, are formed in continuous bands of some depth around the margin of very large thalli in some species of *Porphyra*, and their interpretation as carpospores presupposes that every cell of the region is a potential carpogonium and that every carpogonium is fertilized. Thuret and Bornet (1878) state that such spores may be formed even from cells from which rhizoidal outgrowths have developed, although such cells never undergo vegetative cell division.

Moreover, it is unexpected and without parallel to find spermatia and carpospores formed in an identical manner as would be the case if the spores of Type III of *Porphyra* were accepted as carpospores. Similar arguments apply to *Bangia*. If spores of Type III of *Porphyra* and *Bangia* are not carpospores, however, the different method of germination of spores of Type II and Type III in these genera remains to be explained.

The evidence for considering the spores of Type III of *Porphyra* and *Bangia* as female gametes has been given, and it is obviously insufficient and inconclusive. However, the similarity in formation of these spores and of spermatia, emphasised when both develop from parts of the same mother-cell, supports the interpretation that both are gametes, the one male, the other female.

The third possibility that either all or some of the spores of Type III are asexual should also be kept in mind but appears to have received no serious consideration. The difficulty of distinguishing sexual and asexual spores of *Porphyra* and *Bangia* is referred to in the literature, but both types of spore referred to in these instances are formed in the same way after the first wall has been laid down. It is assumed that the position of the first wall is different if the mother-cell is in fact a zygote, but it has been pointed out already that this distinction does not seem to have been clearly established.

The difficulty of distinguishing the asexually produced spores from spores supposed to be carpospores in *Bangia* is referred to by Reinke (1878, p. 300), Rosenvinge (1909, p. 57), Hamel (1924, p. 4) and Dangeard (1927, p. 194, 205). Hamel states that the best method of distinguishing them is to observe their method of germination. Similarly, Kylin (1946) deduces whether asexual

or sexual thalli of *Porphyra* are present in a given locality from the method of germination of the spores. There is no proof, however, that asexually produced spores germinate in one way and carpospores in another. In fact, Okamura, Onda and Higashi (1920) consider that the type of germination shown by the spores of *Porphyra* depends on external conditions, but, as their figures suggest that the sporelings grown were abnormal, their thesis is not very convincing either.

It will be recalled that in the manner of their formation, these spores of Type III of *Porphyra* are very similar to the spores of *Phragmonema*. Since no spermatia are known in the latter genus, it is concluded that they are asexual.

The observations and figures published would appear to favour the first interpretation, namely, that the spores of Type III of *Porphyra* and *Bangia* are carpospores, but, as has been pointed out, there are serious difficulties in the way of accepting this interpretation. These objections can be removed only by further careful investigations, investigations which will have to provide both undoubted evidence of fertilization, on the one hand, and explanations of the various phenomena previously described as the fertilization act.

Further observations concerning asexual spore formation and re-interpretation of the observations would be of value in classifying the Bangiophycidae. In addition, establishment of the method of sexual reproduction and also of the full life-history of these genera of algae would be of help in indicating the possible affinities of this isolated group of plants. On account of their pigments and because of the general acceptance of Berthold's account of sexual reproduction and post-fertilization developments, they have been referred to by some writers as the Protoflorideae, a name suggesting that they resemble the algae from which the Florideophycidae developed. The evidence available seems insufficient to warrant such a point of view, and even inclusion of the Bangiophycidae as a sub-class of the Rhodophyceae, the other being the Florideophycidae, may suggest a closer relationship than is justifiable.

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ANNOTATED ADDENDA

ARASAKI, S. 1954. On the life history of *Porphyra tenera* Kjellm. Rigaku [Science] **24:** 152. [Eng. abs. Rec. Res., Fac. Agr.; Univ. Tokyo. IV. 1953–1954. Pub. 1955. Item 104].

General remarks on life history.

DANGEARD, P. 1954. Introduction à la Serie XXXVIII Botaniste. Le Botaniste **38:** v–xiv.

Records i) occurrence of *Conchocelis rosea* at Roscoff and in the Bassin d'Arcachon; ii) germination of carpospores of *Porphyra umbilicalis* and penetration of shell by the filaments but differences noted between them and *C. rosea*; so thinks connection with this alga not proved; iii) opinion that growth from carpospores is in the nature of a protonema, not of a phase producing spores; iv) rarity of fertilization tubes in material used, although male thalli present; similarly, carpospores of *Bangia* unrecognisable by fertilization tubes to attached spermatia, although male filaments present; v) germination of spores of *Bangia* which always gave *Bangia* filaments.

OGATA, E. Perforating growth of *Conchocelis* in calcareous matrices.

Date of publication and journal unknown, not on reprint seen. Manuscript received for pub. Dec. 12th. 1955. *Conchocelis*-phases of *Porphyra tenera* and *Bangia fuscopurpurea* grown in thin flakes of calcite and limestone. Fertile cell-rows of *Bangia* developed and later uniseriate upright plantlets appeared on the surface of the calcite, possibly from monospores from the fertile cell-rows.

SUTO, S. 1954. On the life-history of *Porphyra tenera*. III. Bull. Jap. Soc. Sci. Fish. **20:** 494.

The suggestion that carpospores pass the summer in a resting condition and then develop into leafy *Porphyra* thalli, put forward in an earlier paper, is withdrawn. This is as a result of measurements of the spores liberated from the *Conchocelis*-phase of *Porphyra* and of the fact that these spores grow into the leafy thalli.

———— and FUJIYAMA, T. 1952. On the life-history of *Porphyra tenera*. Bull. Jap. Soc. Sci. Fish. **17:** 1.

From measurements of 'autumn spores' and monospores from various sources and also of germlings, it is concluded that the 'autumn spores' are not monospores.

————, MARUYAMA, T., and UMEBAYASHI, O. 1954. On the shedding of spores from "*Conchocelis*-phase" of *Porphyra tenera* cultured in shells of bivalves. Bull. Jap. Soc. Sci. Fish. **20:** 490.

As a result of studying the shedding of spores from the *Conchocelis*-phase of *Porphyra tenera* under laboratory conditions, it was found that this occurs chiefly between 7 and 10 a. m., abundantly in temperatures of 12-22° C. and when the sea-water has a density of 1,023.

TAKEUCHI, T., MATSUBARA, T., SHITANAKA, M., and SUTO, S. 1954. On the shedding of spores from cultured "*Conchocelis*-phase" of *Porphyra tenera* set in the sea. Bull. Jap. Soc. Sci. Fish. **20:** 487.

After the *Conchocelis*-phase of *Porphyra tenera* had been grown in oyster shells, the latter were set in the sea. A certain number of shells were removed daily from the sea and put in glass tubes in the laboratory, and the number of released spores were counted. Large numbers of spores were released during the two to three days of spring tides and small numbers on other days. Shedding of spores took place from late September until early December.

TSENG, C. K. and CHANG, T. J. Studies on the life history of *Porphyra tenera* Kjellm. Scientia Sinica **4:** 375. [date ?]

A combination of two papers published in Chinese in Acta Botanica Sinica **3:** 287 (1954) and **4:** 27 (1955). This paper deals with the dwarf summer thalli and with their significance in the life history, the

morphology of the *Conchocelis*-phase, and the formation and liberation of the spores of the *Conchocelis*-phase. These spores are called "conchospores" and are shown to germinate into leafy *Porphyra* thalli. The evidence provided in support of this last statement appears to be conclusive; thus the gap in our knowledge of that aspect of the life history is closed.

———— and ————. 1955. Studies on *Porphyra*. III. Sexual reproduction of *Porphyra*. Acta Bot. Sin. **4**: 153.

From their own observations, the writers support the statements of Berthold and Dangeard about fertilization and the occurrence of reduction division immediately after fertilization.

———— and ————. 1955. A revision of the life cycle diagram of *Porphyra tenera* Kjellm. Acta Bot. Sin. **4**: 265.

This replaces an earlier diagram by the same authors.

———— and ————. 1956. Conditions of *Porphyra* conchospores, formation and discharge and discharge rhythm. Acta Bot. Sin. **5**: 33.

It is reported that the fertile cell-rows of *Porphyra tenera* are formed at temperatures of from 15° C. (possibly 16-17° C.) to 30° C., but spores are formed in them only after they have been subjected to temperatures of 15-20° C. for a minimum of 11–14 days. Shaking is necessary to induce liberation, which takes place at temperatures up to 25° C. Conchospores may be formed on two-year-old growths at 10° C. Spore discharge takes place early in the morning; the peak is between 8 and 10 a. m., and it almost stops at night. It is considered that discharge is affected by both light and temperature. In a second species of *Porphyra*, although the peak discharge is at the same time, spores are discharged during the afternoon and night also.

YAMASAKI, H. 1954. Studies on the ecology of the *Conchocelis*-phase of *Porphyra tenera* Kjellm. I. Bull. Jap. Soc. Sci. Fish. **20**: 442. [Eng. abs. Rec. Res., Fac. Agr.; Univ. Tokyo. V. 1954-1955. Pub. 1956. Item 78.]

The development of this phase from germination to the adult state with the formation of monosporangia has been followed, especially from the ecological view-point.

————. 1954. Studies on the ecology of the *Conchocelis*-phase of *Porphyra tenera* Kjellm. II. Shedding and fixing of spores. Bull. Jap. Soc. Sci. Fish. **20**: 447. [Eng. abs. Rec. Res., Fac. Agr.; Univ. Tokyo. V. 1954–1955. Pub. 1956. Item 79.]

Spores are liberated from the sporangia on the protonema for two hours after sunrise on bright days but later on cloudy days. Within two minutes of contact with the substratum, they become attached. The highest percentage of attachment occurs immediately after liberation.

EXPLANATION OF PLATES

These plates have been assembled to illustrate the different types of spore formation, the development of spermatia and the various methods of fertilization. The terminology used in the legends is usually that of the investigator, to whose figures they refer.

Plate I. A: *Bangia fuscopurpurea*, after Drew. Formation and release of spermatia. B: *Erythrotrichia tristanensis*, after Baardseth. Formation of spermatia. C: *Erythrotrichia carnea*, after Taylor. Formation and release of monospores (Type I). D: *Porphyridium cruentum*, after Geitler. Two stages in formation of four separate daughter-cells by simultaneous division of mother-cell shown by upper figures, retention of daughter-cells within mother-cell wall by lower figures. E: *Rhodospora sordida*, after Geitler. Autospore formation. F: *Phragmonema sordida*, after Zopf. Filament, the cells of which have each divided to give several spores (Type III). G: *Bangia fuscopurpurea*, after Drew. Formation and release of monospores (Type II). H: *Compsopogon coeruleus*, after Thaxter. Formation of monosporangia from cortical cells (Type I). I: *Porphyra leucosticta*, after Dangeard. Liberation and germination of monospores (Type II). K: *Porphyra umbilicalis* v. *laciniata*, after Drew. Formation of several spores from one mother-cell (Type III).

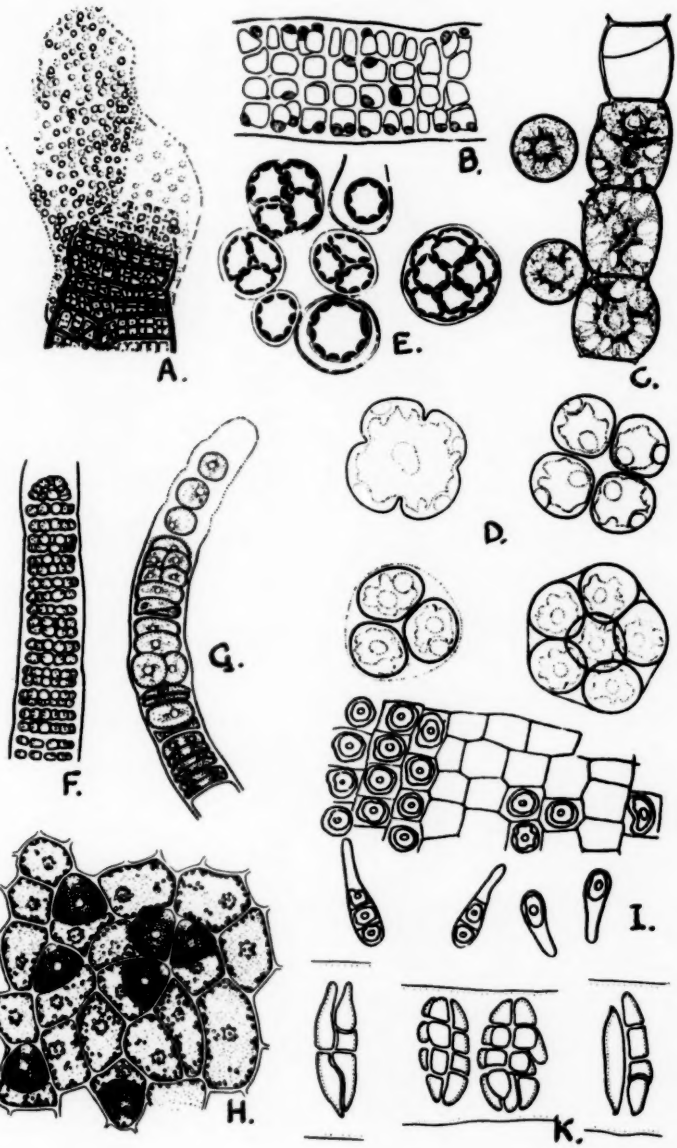
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Plate II. A and B: *Porphyra leucosticta*, after Berthold. Fertilization through a fine canal between the spermatium resting on the outside of the thallus and an unmodified cell of the thallus. C: *Porphyra naiadum*, after Knox. Fusion of sperm and released egg in passage (a) formed between the two; in b the smaller cell is empty. D: *Porphyra laciniata*, after Berthold. Spermatia adhering to the surface of a protruding cell of the thallus, considered to be a fertilized procarp. E, F, G, H, I: *Porphyra* sp., after Joffé. A selection of that author's figures of fertilization. Compare E and F with A and B. In E various stages of the entry of the nucleus of the spermatium into the egg are to be seen. The egg of G also contains two nuclei. In H and I a protrusion of the cell retained in the thallus, called a "trichogyne" by Joffé, is shown engulfing a whole spermatium. K, M, N, O: *Porphyra tenera*, after Kunieda. K: T. S. of thallus, showing cells with two trichogynes each, one on either side. M, N, O: Stages of fertilization by engulfment of the spermatium by the trichogyne, as seen from the surface. L: *Porphyra umbilicalis* f. *linearis*, after Dangeard. Fertilization in a manner similar to that figured by Berthold in A and B. Note the profusion of fertilization canals on both sides of the thallus. Free spermatia lying near by. P: *Porphyra umbilicalis* after Dangeard. Female cell with pseudo-trichogynes, showing at left the penetration of the male nuclei into the protoplasmic papillae.

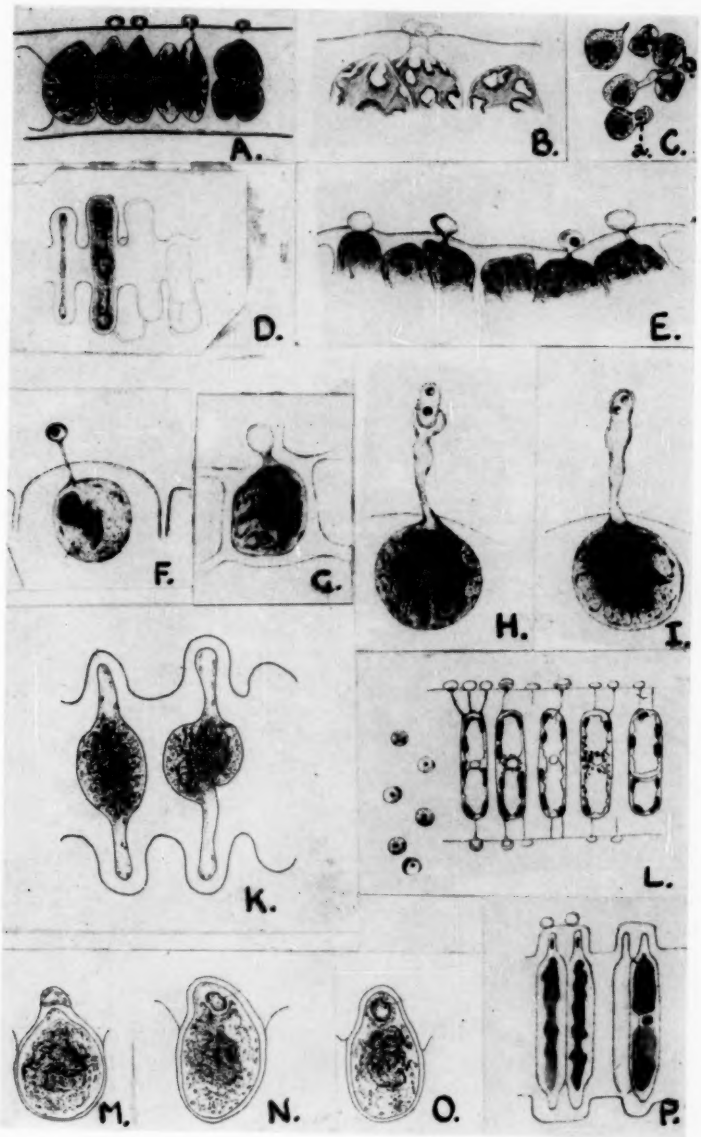
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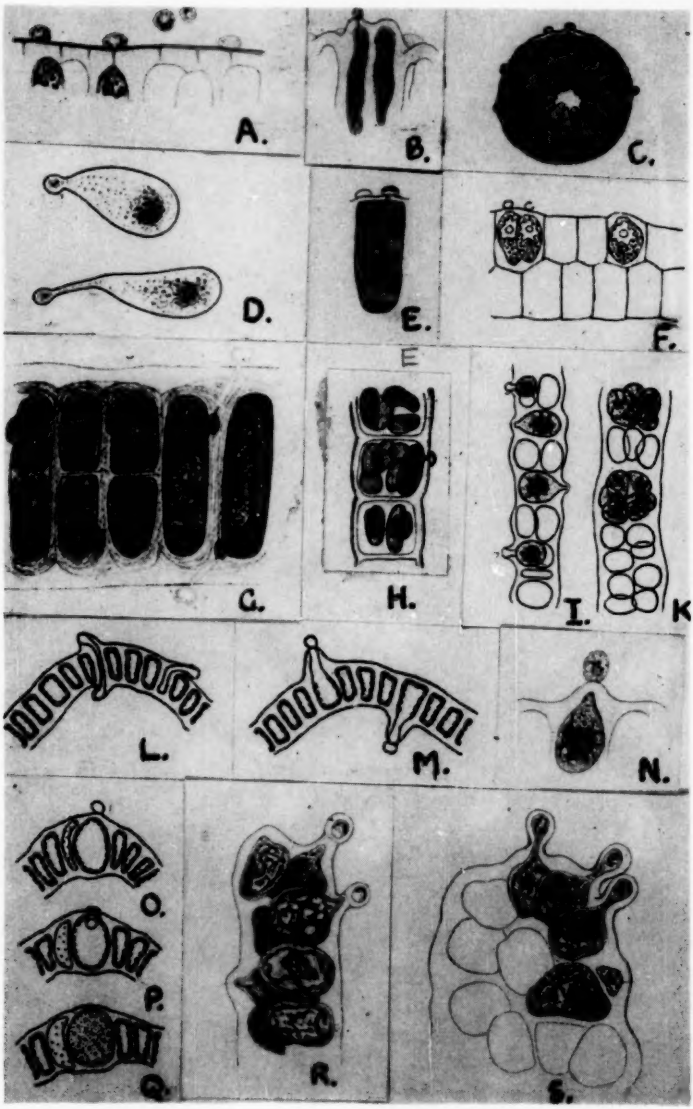
Plate III. A, B: *Bangia fuscopurpurea*, after Berthold. Fertilization through a fine canal connecting the spermatium, which remains on the outside of the thallus, and an unmodified cell within it. C, E, F: *Bangia fuscopurpurea*, after Dangeard. Section of thallus in C, showing fertilization in the same manner as that shown by Berthold. Note two protoplasts within a single cell-wall in F (living material) and also the two nuclei in contact in the cell to the right. In E two nuclei in contact, considered by Dangeard to be the male and female nuclei. D: *Bangia fuscopurpurea*, after Reinke, who considered it possible that this might represent fusion of released female gametes and spermatia. Cf. Pl. II, C. G: *Bangia atropurpurea*, after Schiller. The spermatia appear to have penetrated into the filament and are adpressed against the protoplasts. H: *Bangia pumila*, after Darbishire. The single spermatium is attached to one of a number of spores contained within a single cell wall. I, K: *Erythrotrichia reflexa*, after Tanaka, who considers that I represents part of a female filament with possible cystocarps. L, M, O, P, Q: *Kyliniella* sp. after Flint. Two types of fertilization described by him. For explanation see text. N, R, S: *Erythrotrichia obscura*, after Berthold, who believed that these filaments show stages in the fertilization of cells retained in the thallus. In S the formation of a spermatangium is also to be seen.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Future Contents of

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